1989

# Diel behavior of the apple blotch leafminer moth, Phyllonorycter crataegella (Clemens) (Lepidoptera: Gracillariidae).

Thomas Anthony Green
*University of Massachusetts Amherst*

# DIEL BEHAVIOR OF THE APPLE BLOTCH LEAFMINER MOTH, *PHYLLONORYCTER CRATAEGELLA (CLEMENS)* (LEPIDOPTERA: GRACILLARIIDAE)

A Thesis Presented

By

THOMAS ANTHONY GREEN

Submitted to the Graduate School of the

University of Massachusetts in partial fulfillment

of the requirements for the degree of

MASTER OF SCIENCE

May 1989

Department of Entomology

DIEL BEHAVIOR OF THE APPLE BLOTCH LEAFMINER MOTH,

*Phyllonorycter crataegella* (Clemens)

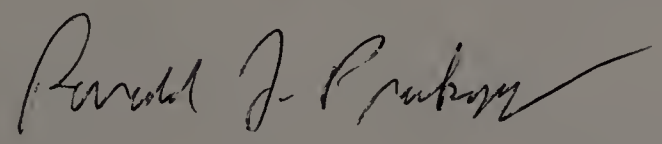
(Lepidoptera: Gracillariidae)

A Thesis Presented

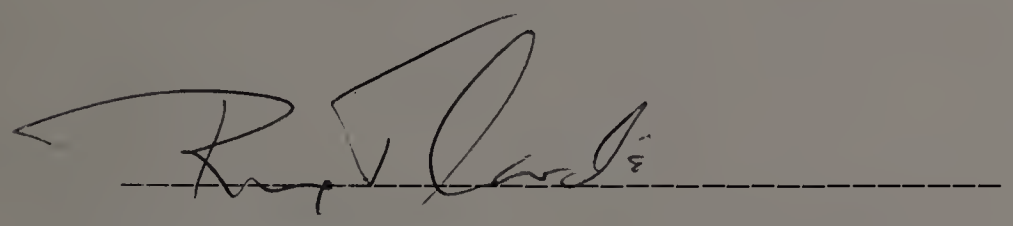
By

THOMAS ANTHONY GREEN

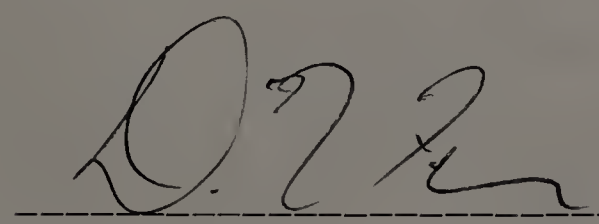
Approved as to style and content by:



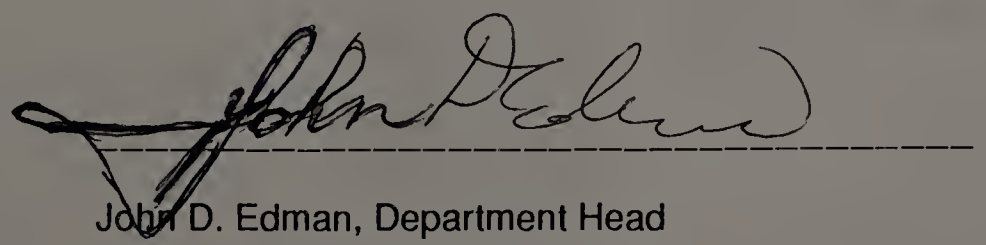
Ronald J. Prokopy, Chairperson of Committee



Ring T. Carde, Member



David N. Ferro, Member



John D. Edman, Department Head

Entomology

## ACKNOWLEDGEMENT

I thank S. Butkewich, G. Hubbell, and M. Rose for excellent technical assistance, and the Atkins, DeLuca, Peck, Rice, Sewall, Shearer, and Smith families for the use of their orchards. I thank R. J. Prokopy for encouragement, advice, and nearly infinite patience.

This research was supported by Massachusetts Agric. Exp. Stn. Project 488, the Massachusetts Cooperative Extension Service, the Massachusetts Society for Promoting Agriculture, and Applied Pest Management Research, Inc.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

# INTRODUCTION

## Literature Review

There are presently at least three major Phyllonorycter (=Lithocolletis) spp. leafminers with similar biology and appearance infesting commercial apple orchards in North America. The apple blotch leafminer (ABLM), *P. crataegella* (Clemens) is an indigenous species found east of the Hudson River and south to Virginia (Beckham et al. 1950, Weires et al. 1980, Maier 1983). The spotted tentiform leafminer (STLM), *P. blancardella* (F.), is an introduced species found in commercial orchards west of the Hudson to Wisconsin (Dutcher and Howitt 1978, Weires et al. 1980, Ridgway and Mahr 1985) and from the Champlain Valley north to Ontario, Quebec, and Nova Scotia (Pottinger and LeRoux 1971, Herbert and McRae 1983). The western tentiform leafminer (WTLM), *P. elmaella* Doganlar and Mutuura is found in western North America (Doganlar and Mutuura 1980).

Other minor gracillariid species have also been noted on rosaceous hosts in North America, including *P. malimalifoliella* (Braun) (Braun 1908) *P. propinquinella* (Braun) (Maier 1985), and *Callisto geminatella* (Pack.) (Beckham et al. 1950, Dean 1963).

The similarities among these species and to other Phyllonorycter spp. have created considerable confusion in the literature, especially prior to 1977. The recent important pest status (ca. 13 years) achieved by ABLM and STLM through the development of resistance to several insecticides (ABLM: Weires 1977, Weires et al. 1982, Van Driesche et al. 1985; STLM: Pree et al. 1980, 1986) has resulted in many published reports on the biology, phenology, behavior, distribution, host range, pest management and bio-control of the ABLM and STLM. These reports have contributed to a resolution of much of the earlier confusion.

The following is an account of the published literature on the ABLM in particular, with reference to related species and emphasis on pest management and those topics

covered by the following chapters. It is the author's intention that this summary and bibliography of the wealth of publications in the past 10 years on the aforementioned diverse range of topics provides a resource to those continuing or considering research on this insect and related or associated species. It is hoped that it provides a view of how scientists from various disciplines, orientations, and geographic locations can cooperatively contribute to a body of knowledge, apply this knowledge, and continue to devise practical approaches to the management of an important pest problem.

## Systematics

The genus Phyllonorycter is placed in the suborder Ditrysia according to the classification of Common (1975). The Ditrysia are thought by Common to be more primitive than other Lepidoptera in that they have two genital openings. Phyllonorycter spp. fall within the superfamily Tineoidea, a primitive group among the Ditrysia.

The ABLM was originally described by Brackenridge Clemens, M.D. (1859) as a univoltine parasitoid of endogenous blackthorn, and later recorded on introduced apple and cherry (Clemens 1861). Clemens (1861) described this insect as having the "unusual habit" of leaving a first mine as a larva and forming a second mine on the same leaf. He probably observed mines of different generations on the same leaf, as ABLM has since been shown to have three complete generations.

STLM was originally described in Europe (Fabricius 1781) and introduced to North America in ca. 1940 (Pottinger & LeRoux 1971). ABLM was redescribed by Braun (1908), and the genus name Phyllonorycter Hubner was reintroduced in place of Lithocolletis Hubner by Bradley et al. (1969). The common name "spotted tentiform leafminer" has been used to describe several species in this genus. Pottinger and LeRoux (1971) suggested that precedence dictates this common name be applied exclusively to STLM, and their suggestion has been largely adopted in the literature since ca. 1978.

WTLM was recently described (Doganlar and Mutuura 1980), and its greater similarity to the Japanese *P. sorbicola* (Kumata) and the European *P. sorbi* (Frey) than to ABLM or STLM was noted.

Biology and Phenology

Beckham et al. (1950) prepared the first detailed description of an insect identified as the spotted tentiform leafminer, *Lithocolletis crataegella* Clemens, now referred to by the common name of apple blotch leafminer (Pottinger and LeRoux 1971). They observed three generations per year, with emergence of the first adults at the pink stage of bud development and continuing through bloom in Virginia.

They reported that female ABLM deposited eggs singly on the undersides of apple leaves (rarely on the upper side), preferentially on the midsection of the leaf. They observed the larva to cut through the eggshell and the lower leaf epidermis and to form a curving linear mine by shearing leaf cells and feeding on the contents. At the third molt, when passing into the fourth instar, a hypermetamorphosis occurred, resulting in the development of chewing mouthparts with which the larva fed on the leaf tissue encircled by the linear mine. This tissue feeding caused the mine to become visible from the upper leaf surface as a spotted blotch. As the larva enlarged the mine, it spun silk which it used to pull the sides of the mine together, creating a tentiform shape. Pupation occurred within the mine, and the adult emerged from the pupal case after poking a small hole through the lower leaf epidermis in which the empty case became wedged.

Beckham et al. (1950) reported an uneven distribution of ABLM moths and mines between trees within an orchard, and a progressive spread of moths and mines upwards in the tree canopy over the three generations. Moths remained primarily on the undersides of apple leaves during the day, with the greatest period of activity and oviposition from mid-afternoon until sundown. They did not report any observations of ABLM mating. Green and Prokopy (1984) confirmed the observations of Beckham et al.

(1950) regarding the distribution of ABLM moths and mines, and the location of ABLM adults during the day. They further reported that mating occurred from first light until mid-morning.

Pottinger and LeRoux (1971), in an extensive life table study of STLM in Ontario, reported a biology similar to ABLM, including three generations and a clumped distribution of moths and mines among trees within an orchard. However, important differences were noted. Oviposition was observed to occur later in the evening than for ABLM (from sunset until darkness) and mating was initiated during this time.

In further contrast to ABLM behavior, Pottinger and LeRoux (1971) observed a uniform distribution of STLM moths and mines throughout the tree canopy in all generations, and attributed this to a uniform resettling after the evening flight period. Moths were observed being blown away from the host during periods of high winds. Males emerged prior to females. Feeding upon a sugar solution increased longevity and fecundity of females by about 50%.

A recent development has been the discovery of a summer diapause in a portion of some Ontario STLM populations, apparently caused by parasitism splitting these populations into two groups (Laing et al. 1986a). One group was found to develop rapidly through the second generation larval stages, emerging as adults in August and proceeding through a final third generation before overwintering as pupae. The other group exhibited marked delayed development of early instars of the second generation, which then overwintered as second generation pupae. This delayed development apparently resulted in little parasitism by Sympiesis sp., ectoparasitoids of fourth and fifth instar STLM and ABLM. This phenomenon has not been reported in ABLM.

Oviposition Behavior

Beckham et al. (1950) found oviposition by ABLM in Virginia to occur from mid-afternoon until sundown. When caged individually, female ABLM in sleeve cages on apple

foliage outdoors oviposited a total of 10.8-16.0 eggs each, almost exclusively on the leaf undersides. These females apparently preferred the mid-section of the leaf, although no quantitative information was presented. Larval mines were concentrated in the lower part of the tree in the first generation, being found higher in the tree in subsequent generations in this and a more recent study (Green et al. 1985).

Pottinger and LeRoux (1971) reported oviposition by STLM to occur from ca. 1950 to 2400 hours EST in Quebec. Oviposition always occurred on the underside of the leaf, and consisted of touching the ovipositor to the leaf surface several times before there was a violent shaking of the abdomen back and forth 4-5 times and deposition of an egg. The mean time from first ovipositor contact with the leaf surface to egg deposition was 27.3 s. Egg production was positively correlated with longevity, with a mean of 21.6 eggs laid per individually-caged female in sleeve cages on apple foliage outdoors. The provision of a sugar solution increased longevity from ca. 4 to 11 days, and lifetime fecundity from ca. 22 to 57 eggs, over females provided with water only. The number of eggs laid per day (ca. 4.6) did not increase. These results suggest the availablility of carbohydrate may limit STLM fecundity in the field.

Trimble (1984) reported results partially contradictory to those of Pottinger and LeRoux. STLM females maintained in the laboratory and provided with sugar solution lived longer, but were no more fecund, than females provided with water only (mean 35-42 total eggs per female). Trimble (1986) estimated the threshold temperature for STLM oviposition in the field to be ca. 9 C.

Geographic and Host Ranges

Early reports of a "spotted tentiform leafminer" infesting apple in western N. Y. State (Brunn 1883), eastern N. Y. State (Dean 1940), and Virginia (Beckham et al. 1950) must have been of ABLM, if the 1940 introduction date for STLM was correct (Pottinger and LeRoux 1971). Due to the confusion in the pre-1970's literature in

distinguishing ABLM, STLM, and related species, Pottinger and LeRoux (1971) suggested it would be impossible to determine positively the geographic distribution of particular species prior to 1970.

The first systematic attempt to define the geographic range of STLM and ABLM was by Weires et al. (1980) and Weires (1981). These authors reported that STLM were present in commercial orchards west of the Hudson River and in the Champlain Valley of N. Y. and Vermont. ABLM was reported in the Hudson River Valley, on both sides of the river, and east in Massachusetts and Connecticut. In these and subsequent reports, the two pair of cremastral hooks on the pupae have been used to distinguish these species. The inner pair are smaller than the outer pair for ABLM, whereas those of STLM are of equal size.

Maier (1983) clarified this picture by reporting that ABLM was dominant in sprayed apple orchards in Connecticut and in unsprayed apple trees near commercial orchards, but that STLM predominated in unsprayed sites not adjacent to commercial apple orchards. Maier found primarily STLM in only one commercial apple orchard in northwestern Conn., but in subsequent years ABLM has become the dominant Phyllonorycter species at this site as well (Maier pers. comm.).

In Mass., Van Driesche and Taub (1983) obtained results similar to Maier's, with ABLM dominant in commercial apple orchards and in unsprayed apple trees within 0.5 km of commercial orchards, and STLM dominant on apple at other sites.

STLM has been reported in commercial orchards in Michigan (Dutcher and Howitt 1978), Wisconsin (Ridgway and Mahr 1985), Ontario (Pottinger and LeRoux 1971, Johnson et al. 1976), and Nova Scotia (Herbert and McRae 1983).

WTLM, apparently misidentified as *Lithocolletis crataegella* by Wilson (1915) and as Lithocolletis sorbi Frey by Pottinger and LeRoux (1971), has been recorded from British Columbia and Oregon (Doganlar and Mutuura 1980), Washington State (Hoyt 1983) and Utah (Barrett and Jorgensen 1986).

The host ranges of ABLM and STLM were compared in Connecticut and found to differ considerably (Maier 1985). ABLM was found to exhibit a polyphagous host range, completing development on 17 native and exotic rosaceous hosts including Malus and Prunus spp. STLM was apparently restricted to introduced Malus spp., including apple and wild crab. This is in contrast to the host range of STLM in Europe, which includes a wide range of species in 7 genera, including Malus, Prunus, Pyrus, and Crataegus (Maier 1985).

Pest Management

Periodic outbreaks of ABLM have occurred since 1939 throughout its geographic range, including N.Y. (Dean 1940, 1963; Weires 1977, 1981; Weires et al. 1977), Virginia (Beckham et al. 1950), and New England (Maier 1981, Coli and Prokopy 1982). Prior to 1977, nicotine sulfate, lead arsenate, DDT, DDE, parathion, malathion, azinphosmethyl, phosphamidon and various combinations of these materials were recommended in pink or cover sprays to control ABLM (Dean 1940, 1963, Beckham et al. 1950).

In 1977, the failure of organophosphate insecticides to control ABLM in Hudson Valley orchards was reported, and methomyl, demeton and chlordimeform hydrochloride were recommended (Weires 1977). Weires advised growers to assess the need for a control measure by monitoring first generation mines, and to treat only if the number of mines exceeded 0.2 per fruit cluster. Oxamyl, endosulfan, and formetanate hydrochloride were added to the list of recommended materials in 1981, and the threshold for treatment was revised to 1.0 mines per leaf in the first generation (Weires 1981).

Impressions of premature fruit ripening and drop were reported for trees heavily infested with STLM (Pottinger and LeRoux 1971). A number of different types of economic injury including premature fruit ripening and drop, reduced fruit size and

firmness, and reduced fruit production and set the following year was confirmed at second-generation ABLM larval densities ranging from 2-4 mines per leaf, depending on the cultivar (Reissig et al. 1982).

Increased injury was noted where caustic sprays were applied to leaves heavily infested with ABLM (Beckham et al. 1950, Coli and Prokopy 1982), or where older, less vigorous trees were infested (Reissig et al. 1982). A reduced treatment threshold of 0.13 mines per leaf in the first generation was proposed in Massachusetts in consideration of these factors and other stresses such as drought or mite injury (Coli and Prokopy 1982). Growers were advised to apply insecticides against ABLM on warm, calm evenings in early spring to coincide with maximum oviposition activity by ABLM (Green et al. 1985).

The desirability of insecticide treatments before bloom to preserve beneficials was cited (Weires 1981, Coli and Prokopy 1982). This recommendation was based on the toxicity of many of the newly recommended materials to mite predators (Hislop and Prokopy 1981), which do not appear in apple trees until after bloom (Hislop and Prokopy 1979). However, no reliable means of determining the need for a treatment prior to the appearance of mines had been reported. Attempts to correlate third generation larval density with the next year's first generation population proved inadequate (author, unpublished data), probably due to variation in orchard floor wetness, snow cover, predation, wind dispersal of infested fallen leaves over the winter, and to leaf burial by earthworms prior to adult leafminer emergence in the spring (Laing et al. 1986).

An attractant has been identified for STLM males (Roelofs et al. 1977), and is commercially available. This lure has not proved effective in attracting ABLM (Weires et al. 1980), and no correlation exists between trap captures and ABLM mines per leaf in Massachusetts commercial orchards (Coli and Prokopy 1982). A sticky red visual trap was developed in Massachusetts to predict the need for an insecticide treatment

against ABLM before bloom, based on the number of ABLM adults captured (Coli and Prokopy 1982, Coli et al. 1985, Green and Prokopy 1984, 1986). During 1985 and 1986, this trap was used to predict accurately the need for an insecticide treatment in 13 of 14 commercial orchard blocks where no insecticide was applied for ABLM before bloom so as to allow observation of trap captures and subsequent larval mines per leaf (Green et al. 1987).

Alm et al. (1985) investigated apparent resistance of certain apple cultivars to STLM. They found ABLM completed development on all cultivars tested, including one Malus sp. observed by Pottinger and LeRoux (1971) to escape STLM infestation. Alm et al. suggested that this and other species noted by Pottinger and LeRoux may not produce foliage early enough in the season to permit infestation by first generation STLM. Alm et al. did confirm an oviposition preference by female ABLM adults for Macspur, and against Malus fusca, the Oregon crab.

Weires and Forshey (1978) speculated that outbreaks of tentiform leafminers in N. Y. may have been the result of resistance to organophosphate insecticides. They noted that if parasitoids and predators of ABLM remained susceptible to commonly used orchard pesticides, leafminers would be released from both chemical and natural controls in commercial orchards.

This speculation was confirmed, as both resistant ABLM and STLM populations were identified in commercial orchards in N. Y. (Weires et al. 1980, 1982). Resistance to organophosphate insecticides was reported for ABLM in Massachusetts (Van Driesche et al. 1985), and for STLM in Ontario (Pree et al. 1980). The development and spread of resistant leafminer populations may have been enhanced by repeated and universal use of predominantly organophosphate insecticides in commercial orchards (7-10 applications per season, Coli et al. 1983), by exposure of three generations of leafminers per season to insecticide selection for resistant individuals, by lack of sufficient immigration of susceptible individuals into commercial orchards due to parasitoid regulation of

populations in unsprayed trees, and by the movement of pupae in apple leaves in bins of harvested apples from one region to another.

Resistance to pyrethroid insecticides has been reported for STLM in Ontario after 4-5 seasons of use, and it has been speculated that this may involve cross- resistance, with re-selection of a DDT resistant strain (Pree et al. 1986).

A chitin synthesis inhibitor, diflubenzuron, not yet available for commercial use on apple, may provide excellent control of ABLM in the future (Green et al. 1987).

Bio-control

Dean (1940) was apparently the first to note the importance of parasitoids in controlling ABLM. Beckham et al. (1950) found greater than 50% parasitism of ABLM larvae in commercial orchards in Virginia. Pottinger and LeRoux (1971) reported parasitism to be the primary mortality factor regulating STLM populations in several unsprayed apple orchards in Ontario during the growing season. They observed numerous predated bodies of STLM adults, associating this with the presence of many jumping spiders.

Coli and Prokopy (1982) observed 24% parasitism of ABLM larvae in commercial orchards vs. 83% at unsprayed sites. They reported 100% mortality to ABLM parasitoids (but 0% to ABLM adults and larvae) from applications of azinphosmethyl and phosmet. A reduction in insecticide application has been correlated with a large increase in parasitism in commercial orchards (Maier 1982), resulting in excellent control in some cases (Prokopy 1985).

Recent research on biological control of ABLM has focused on identification of important beneficial species, determination of phenologies to time insecticide treatments to spare beneficials, and insecticide toxicology to identify materials most toxic to ABLM and STLM and least toxic to beneficials.

A diverse fauna has been found to parasitize ABLM and STLM, apparently a common phenomenon in Phyllonorycter sp. leafminers (Askew and Shaw 1979). A pattern for STLM in many areas is the dominance of a braconid endoparasitoid *Pholetesor* (=Apanteles) *ornigis* (Weed) (PO), , during the first and third generations (Johnson et al. 1976, 1979, Dutcher and Howitt 1978, Maier 1984, Ridgway and Mahr 1985). Although some reports have described PO as parasitizing fourth and/or fifth instar leafminer larvae (Beckham et al. 1950, Pottinger and LeRoux 1971, Gambino and Sullivan 1982), recent evidence suggests that only first through third instars receive eggs from PO (Ridgway and Mahr 1985, Laing et al. 1986).

*Sympiesis marylandensis* Girault (SM), a eulophid ectoparasitoid of fourth and fifth instar leafminer larvae, was found to dominate during the second generation in the preceeding studies. Host feeding on early instar leafminers, and/or lethal "stinging without oviposition" by SM adults have also been observed (Pottinger and LeRoux 1971, Van Driesche and Taub 1983, Ridgway and Mahr 1985). Phenological differences and hyperparasitism of PO by SM probably largely accounted for the alternating dominance of SM with PO, possibly in combination with apparent greater susceptibility of PO than SM to organophosphate insecticides (Hagley et al. 1981, Maier 1982). Lethal residues of these insecticides are usually no longer present by the time third generation leafminers are in susceptible instars (September onwards).

This common pattern of STLM parasitism apparently does not exist with ABLM, as studies in sprayed orchards have indicated a dominance of SM in the first generation (Gambino and Sullivan 1982) or in all three generations of ABLM (Weires et al. 1980, Maier 1982, Van Driesche and Taub 1983).

In addition to the presence of dominant parasitoid species, numerous other parasitoid and predator activities have been reported to impact leafminer populations including: feeding on eggs (Beckham et al. 1950) or larvae (Ridgway and Mahr 1985) by Chrysopa sp.; feeding on larvae by a plant bug, *Hyaloides vitripennis* (Say) (Beckham et al.

1950); ectoparasitism, hyperparasitism or feeding on larvae by numerous Eulophid sp. including *Sympiesis conica* (Provancher) and *Pnigalio maculipes* (Provancher) (Pottinger and LeRoux 1971, Weires et al. 1980, Gambino and Sullivan 1982, Maier 1984); and burial of leaves containing leafminer pupae by the earthworm, *Lumbricus terrestris* L. (Laing et al. 1986).

The phenologies of ABLM and STLM, and of SM and PO spring emergence, have been assessed to determine a "biological window" during which insecticides may be applied selectively to control leafminers with the least harm to beneficials. SM has been found to emerge in approximate synchrony with STLM and ABLM, while PO has been found to emerge 10-30 days later (Johnson et al. 1976, Gambino and Sullivan 1982, Herbert and McRae 1983, Maier 1984, Drummond et al. 1985). Herbert and McRae (1983) and Johnson et al. (1979) built temperature-dependent emergence models for STLM and its principal parasitoid, PO. Both models predicted an optimum time for application of insecticide to preserve PO based on emergence dates. A model was also constructed for ABLM and SM which indicated that timing to preserve SM may not be possible in all years due to the closely matched time of emergence (mean peak emergence difference between ABLM and SM is only 4.5 days, Drummond et al. 1985).

Selective choice of insecticides has been investigated to preserve leafminer parasitoids. In Massachusetts, oxamyl has been shown to be more toxic to ABLM than to SM (Van Driesche et al. 1985). In Ontario, permethrin was found to be 9 times more toxic to STLM than to PO (Hagley et al. 1981). Both of these materials have disadvantages. Oxamyl is highly toxic to mite predators, while resistance to permethrin has been demonstrated after just 4-5 years of use.

A final avenue of approach to biological control of leafminers evident in the literature is the successful introduction of an exotic parasitoid of STLM, *Pholetesor pedias* (Nixon), into Ontario from New Zealand (Laing and Heraty 1981). Within three

years, two individuals had multiplied sufficiently to increase STLM mortality by 20% without supressing PO parasitism, and *P. pedias* was found as far away as 43 km from the release site. An interesting note is the apparent transformation of *P. pedias* into a uniparental strain following its introduction.

## Conclusion

The substantial number of gracillariid leafminers with similar biologies and appearance infesting apple all over the world raises questions as to their evolutionary past and present. Interesting issues to be investigated include common ancestry, possible convergent evolution, genetic distance, and host shifts. Apparently ABLM has been able to shift to various roseaceous species introduced into North America, but STLM has yet to colonize many potential endogenous hosts.

The interesting geographic distribution of ABLM and STLM, including regions of apparent allopatry and sympatry as well as segregation partly according to orchard management practices, raises the question of which factor(s) might be responsible for this observed pattern. Possibilities include competitive exclusion and interspecific differences in such factors as climactic tolerance, host preferences, pesticide susceptibility, parasitoid and predator fauna, and oviposition and mating behavior. This situation presents opportunities for the examination of potential character displacement and contact zone formation and movement.

Patterns of inter- and intraspecific distribution, host preferences, aggregation within and between trees in orchards, and the apparent selection of a particular portion of the leaf for oviposition by ABLM females suggest the possibility of inter- and/or intraspecific competition in STLM and ABLM. Competition has been demonstrated in homopterans (McClure and Price 1975), dipteran leafminers (Potter 1985, Quiring and McNeil 1984), and lepidopteran leafminers (Martin 1956, Bultman and Faeth 1985). Various mechanisms have evolved in different taxa, including the Lepidoptera,

which influence spacing and regulate competition for resources (Prokopy 1981, Prokopy et al. 1984). The importance of inter- and intraspecies competition, and the potential existence of resource partitioning mechanisms, have yet to be examined for ABLM or STLM.

The objective of the following study was to shed light on some of these questions, and to add to the knowledge base which can be applied to the management of these pest species. Specifically, the diurnal pattern of ABLM adult behavior in commercial apple orchards in New England (Chapter I) and the oviposition behavior of ABLM females in the laboratory (Chapter II) were observed in detail.

# CHAPTER 1

## DIEL BEHAVIOR OF THE APPLE BLOTCH LEAFMINER MOTH *PHYLLONORYCTER CRATAEGELLA* (LEPIDOPTERA: GRACILLARIIDAE)


Abstract

Observations of apple blotch leafminer moths, *Phyllonorycter crataegella* (Clemens), during daylight hours in commercial apple orchards in New England from 1981 through 1984 indicated a diel pattern of activity. Substantial flight in the morning (0700-1100 DST), almost exclusively by males, was associated with mating, and lesser flight in the late afternoon through darkness (1500-2100), predominantly by females, was associated with oviposition. Moths were inactive throughout midday, and were located primarily on the lower third of the tree trunk during the first (spring) generation, and on the undersides of leaves during the second and third (summer) generations. Moths and larval mines were concentrated in the inner half of the tree canopy during both spring and summer generations, and especially below 1.5 m height during the first generation.


Introduction

The apple blotch leafminer (ABLM), *Phyllonorycter crataegella* (Clemens), has recently become a serious pest in commercial apple orchards in the northeastern United States (Weires et al. 1980, Van Driesche and Taub 1983, Maier 1983).

The ABLM completes 3 generations per year in this region, overwintering as pupae in fallen leaves on the orchard floor. Adults are present from late April to mid-May,

from mid-June to mid-July, and from early August to early September during the first, second and third generations, respectively (Maier 1981, Coli and Prokopy 1982). Female ABLM deposit eggs singly on the undersides of apple leaves. Hatched larvae form mines between the upper and lower leaf epidermal layers, resulting in a variety of injuries to the crop (Reissig et al. 1982).

Previously, Green and Prokopy (1986) reported on the development of a visual monitoring trap for this pest. In a concurrent investigation, the results of which are reported here, systematic observations were conducted to determine the location and activity of ABLM moths from first light until darkness and over all 3 generations. These observations were carried out on apple trees within (and on non-host trees adjacent to) commercial orchards.

## Materials and Methods

This study was conducted in 6 commercial apple orchards in Massachusetts and 1 in southeastern New Hampshire during 1981 to 1984. Trees were 15-40 year old standard McIntosh, Delicious or Macoun. To avoid immediate influence of insecticide treatments, orchard blocks in which no treatment would be applied against ABLM adults during the generation under study were selected. Insecticide treatments against larvae often necessitated a move to a different orchard for study of subsequent generations within a single year. For observations conducted within individual trees, a minimum of 8 trees was selected within each orchard, and no single tree was used for observation more than twice in any 24-h period.

On 6 and 11 days during the second and third moth generations, respectively, in 1981, 1982 and 1983 (Table 1, experiment 1), various structures within and beneath single trees were inspected visually for the presence of ABLM moths. These structures included ground cover under the tree canopy, undersides of leaves, top sides of leaves, tree trunk, and fruit. In addition, numbers of ABLM in flight were observed while

standing 0.5 m outside of and facing the tree canopy. Each of these locations was inspected for 1 minute (timed with a stopwatch) during each hour observations were conducted. The numbers of ABLM present were recorded. Mating pairs were noted separately and included in the total ABLM observed as 2 individuals. All observations were made from the ground. As much area as possible was inspected carefully during each minute.

Ground cover varied among the orchards studied, and included orchard grass, clover, dandelion, poison ivy, nettles, and wild blackberry and raspberry. To minimize disruption of ABLM behavior, the tree canopy was first observed for flight activity, then the ground cover was observed, then undersides of leaves, etc. Visual surveys were attempted during darkness using a flashlight with a Wratten gelatin filter (No. 29, Eastman Kodak Co.. Rochester, N. Y.) to eliminate light below 600 nm. However, it was not possible to observe surface area equivalent to that observed during daylight, and ABLM appeared to be disturbed by the light even with the filter. Hence, it was not feasible to collect meaningful visual observation data on ABLM behavior during darkness (ca. 30 min after sunset to 30 min before sunrise).

On 8 days during the third generation of 1982 and 5 days during the second generation of 1983 (Table 1, experiment 2), ABLM were captured in flight with a sweep net, or aspirated immediately after landing. Captured moths were sexed in the laboratory. These collections were conducted in apple trees at least 2 rows away from visual survey trees to reduce interference with taking visual count data.

On 7, 9, and 2 days of the first through third generations, respectively, during 1983 and 1984 (Table 1, experiment 3), 1 minute visual surveys were conducted (as in experiment 1) of flight, ground cover, trunk, top sides of leaves, undersides of leaves, and twigs and branches on non-host trees within 20 m of commercial apple orchards. Non-hosts surveyed included pine, maple, poplar, sumac, oak, and beech.

On 7 and 10 days during the first and second generations, respectively, during 1983 and 1984 (Table 1, experiment 4), individual ABLM were observed on apple trees for 5

min periods throughout the daylight hours. An area within the tree canopy was selected at random. The undersides of leaves were searched within that area until an ABLM moth was located. The underside of leaves was selected over other structures, because preliminary results showed this to be the primary location of ABLM throughout the day. The activity of each moth was recorded as oviposition, crawling only, crawling and flying or flying only, in copula, or no movement detected. Oviposition activity was defined as the probing of the leaf underside with the ovipositor and/or the deposition of an egg.

On 7, 4, and 2 days during the first, second and third generations, respectively, in 1984 (Table 1, experiment 5), further 1-min visual surveys were conducted of portions of the apple tree canopy, tree trunk, and ground cover to determine the distribution of ABLM within those areas. The undersides of leaves were observed for 1 min in each of the following 5 areas: below 1.5 m height in the inner half of the canopy; below 1.5 m height and in the outer half of the canopy; between 1.5 m and 2.5 m height and in the inner and outer halves of the canopy; and within 1.5 m of the tree top. The tree trunk was inspected below 1.5 m height, between 1.5 and 2.5 m height, and within 1.5 m of the tree top. The ground cover was observed outside of the tree dripline, under the outer half of the tree canopy, and under the inner half of the canopy. The entire canopy was also observed for ABLM in flight, as in experiment 1. Average tree height was ca. 4-5 m.

Also in 1984, apple leaves were sampled for ABLM larval mines in each of the 5 tree canopy areas just described (Table 1, experiment 6). Ten leaves were sampled from each area in 8 trees for first generation larval mines and in 13 trees for second generation mines. Due to an insecticide application against second generation larvae in the orchard sampled for first generation mines, second generation mines were sampled in 2 separate blocks of a different orchard.

On all days during which the above observations were made, temperature, humidity, average wind speed, and light intensity were recorded hourly throughout observation

periods. Wind speed was measured with a cup anemometer (model W164-B/M, Weather Measure Corp., Sacramento, Calif.) placed at ground level between rows of trees in the orchards. Light intensity was measured with a light meter (Panlux model, Gossen, W. Germany) held horizontally, sensor facing upwards, at 1.5 m height and 0.5 m from the observer while facing away from the tree canopy at the north, east, south and west points of the tree dripline. These 4 readings were then averaged to obtain an hourly value for light intensity.

All data from hourly observations were averaged over 2-h intervals to reduce sampling variation and simplify presentation. Values (N) are reported for the number of minutes each location was observed per 2-h interval within a generation. Multiplying this value by the average number of moths observed per minute during a 2-h period gives the total number of moths observed during that period for that generation (or all 3 generations, Fig. 2). Statistical analyses were conducted on the University of Massachusetts mainframe computer (Control Data Corp. 175), using BMDP statistical software (Dixon 1983).

## Results

Non-mating first generation ABLM were located primarily on the lower third of apple tree trunks (Table 2). Fewer moths were observed on the undersides of leaves and in the ground cover. In contrast with these results, during generations 2 and 3 the leaf underside was the primary location of ABLM individuals, followed by the tree trunk (Tables 2,3). Considerably fewer moths were observed on fruit, ground cover, or top sides of leaves in any generation.

No mating pairs were observed during surveys of the tree trunk or ground cover during the first generation (Table 3). However, it was extremely difficult to spot ABLM among the matted dead grass and leaves in the ground cover without disturbing them. Due to the fact that first-generation adults emerged from overwintering fallen leaves, the

number of moths (and mating pairs) located in the ground cover during the day undoubtedly was substantially greater than we were able to detect. Several mating pairs were observed on the tree trunk and in the ground cover at times other than during 1-min surveys.

On average, during the first generation the distribution of ABLM adults on the undersides of leaves (Tables 2, 4), and the distribution of larval mines (Table 4) favored the inner half of the canopy, especially below 1.5 m. ABLM spread upwards in the second generation, but continued to be concentrated in the inner half of the canopy. This concentration continued for ABLM adults in the third generation (Table 2).

No clear diel pattern of ABLM distribution among the tree canopy areas was evident for any generation (Table 2). Overall, however, the numbers of ABLM on the undersides of leaves during the first generation decreased sharply in the early to late afternoon, and increased again from 1700-1900 hours (Table 2). Numbers of ABLM on leaf undersides during the second and third generations increased throughout the day before dropping off prior to (1982-1983, Table 3) or during (1984, Table 2) the evening flight period (1700-1900 hours). Temperature and humidity were consistently lower, and wind speed was considerably greater throughout the day during the first generation compared to the second and third generations (Table 2).

Flight activity was low in the first generation in comparison to the second and third generations (Table 2), especially in the evening. This was also apparent in our 5 min observations of individual ABLM (Fig. 1A, B), which showed a much greater proportion of first generation than second generation ABLM walking in the evening. A peak in the proportion of first generation moths observed in flight occurred between 1100 and 1300 hours.

Flight activity peaked between 0700 and 0900 hours during generations 2 and 3, with a second, usually lesser peak occurring from 1700-2100 hours (Tables 2, 3). These morning and evening periods of peak flight activity corresponded to peak mating

and oviposition periods, respectively (Fig. 1), and to periods of lowest temperature, wind speed, and light intensity, and highest humidity (Tables 2, 3). ABLM captured in flight or immediately post-flight were almost exclusively males in the morning, and predominantly females during the late afternoon and early evening (Table 5).

The diel pattern of activity other than flight was consistent across generations. Mating began between 0500 and 0700 hours, and ceased by 1300 hours (Tables 2, 3). Oviposition began between 1500 and 1700 hours, and increased through 2100 hours in both the first and second generations (Fig. 1A, B). Detailed observations of oviposition behavior recorded during experiment 4 of this study are reported in Chapter 2.

The lowest temperature at which a mating pair was observed was 7o C (RH 58%) on May 10, 1984 (during a systematic survey taken while seeking study sites), on the lower third of the tree trunk. The lowest temperature at which oviposition was observed was 15 oC, (RH 29%) on May 17, 1984 when 3 ovipositing females were recorded.

A similar diel pattern of flight activity and moth location was found on non-host trees adjacent to the orchards, although numbers of ABLM adults were substantially fewer than found on apple trees (Fig. 2). Due to the comparatively low numbers of ABLM observed on non-host trees adjacent to orchards (no ABLM were observed there during 77.5% of 2-h observation periods vs. 10.4% for orchards), and due to the lack of any apparent differences between generations in the data collected from non-host trees, data from all 3 generations were combined for presentation (Fig. 2). Flight activity on non-host trees peaked between 0700 and 0900 hours, with a secondary peak between 1500 and 2100 hours. The underside of leaves was the primary location of ABLM adults throughout most of the day on non-hosts. During a total of 546 min of observation on non-hosts, no ovipositing females and only 3 mating pairs were observed, all on the undersides of leaves.

Discussion

The leafminers observed in this study are presumed to have been ABLM, and not spotted tentiform leafminer (STLM), *Phyllonorycter blancardella* (F.). Previous work has shown ABLM to be the predominant species in commercial orchards in Massachusetts (98.8%, Van Driesche and Taub 1983), Connecticut (91.8%, Maier 1983) and New Hampshire (C. Bartholemew, pers. comm.). This of course does not preclude the possibility that some individuals observed may have been STLM.

The data reported here agree with visual trap data reported previously by Green and Prokopy (1986). They found the majority of captures on red sticky-coated rectangles (20 x 30 cm) hung horizontally (sticky side up) in the canopy of apple trees in commercial orchards occurred between sunrise and 1100 hours and between 1500 and 2100 hours. Trap-captured ABLM were almost exclusively males in the morning and predominantly females in the evening.

The results of this study also confirm several observations of Beckham et al. (1950), who found ABLM were located primarily on the undersides of apple leaves throughout midday and oviposited from mid-afternoon to sundown. Beckham et al. found that ABLM adults (measured by captures in bait pails placed at various positions in the canopy of apple trees) and larval mines were concentrated in the lower part of the canopy in the first generation and spread upwards in the two succeeding generations. They did not report any observations of mating.

Pottinger and LeRoux (1971) reported somewhat different results for STLM than those obtained here for ABLM. They observed STLM both to oviposit and mate in the evening, and found STLM were evenly distributed throughout the tree canopy for all 3 generations. They attributed this even distribution to uniform resettling after the evening flight period.

Beckham et al. (1950), Pottinger and LeRoux (1971), and Green and Prokopy (1986) all noted an apparent cessation of flight and oviposition activity at darkness.

STLM remained in copula until midnight (Pottinger and LeRoux 1971), but there was no suggestion in the literature or in the few observations attempted here that important activity occurs after darkness. In ABLM, females apparently initiate pheromone "calling" only during and after sunrise (T. A. Green, unpublished data).

The adaptive significance of the temporal partitioning of behavior noted in this study may be associated with environmental conditions observed. Oviposition, mating, and flight all occurred during periods of high humidity and relatively low temperature and wind speed. All 3 conditions may be important to ABLM in regulating water loss, but wind speed may be particularly important. Pottinger and LeRoux (1971) noted STLM in flight and on foliage being blown away from the host tree in high wind. They suggested that this was an important mortality factor in that such STLM may not have been able to relocate a host.

Martin (1956) reported non-hosts of the aspen blotch leafminer, *Phyllonorycter salicifoliella* (Chambers), provided shelter from adverse conditions, including high winds, and that alders were more heavily infested with *P. salicifoliella* the nearer they were to non-host conifers. This suggests non-host trees may influence ABLM population density. No other important role for non-hosts is suggested by our study.

Beckham et al. (1950) suggested the progressive spread of ABLM upwards in the tree canopy over succeeding generations was related to proximity to emergence location, as overwintering generation adults emerge from pupae in fallen leaves in the ground cover, and adults from subsequent generations emerge from leaves in the tree canopy. Results of this study indicate the inner half of the tree canopy is the primary location of ABLM adults through all three generations and of oviposition sites through at least the second generation (Tables 3, 4). Ovipositing ABLM were often observed to cease movement and crouch closer to the leaf surface as a gust of wind arose, and to resume activity once it passed. The inner part of the canopy may be the most sheltered from the wind, and thus allow more continuous oviposition activity, resulting in increased larval

density in this region. Alternatively, differences in nutrient or noxious compound concentration, exposure to sunlight (Faeth et al. 1981), or rates of leaf abscission (Bultman and Faeth 1986b) may influence oviposition site choice.

Any influence of wind would likely have been greatest in the spring, when apple foliage was much less profuse than in the summer, and when average wind speeds were substantially greater, at least as recorded in this study (Table 2). If we presume ABLM in flight were more susceptible to wind dispersal, then ABLM avoidance of wind greater than ca. 2-3 kph may have been a principal reason why walking was more prevalent than flight during the oviposition period (1500-2100 h) of the first generation relative to the second generation (Fig. 1), and why first generation ABLM left the tree canopy at midday (Table 2). Evening temperatures were lower in the first generation (Table 2), and this also may have been responsible for decreased flight activity during the evening oviposition period.

The tree trunk may have served as shelter from the wind and as a heat sink, providing an opportunity for basking. This could explain, at least in part, why ABLM were greater in number on the lower third of the tree trunk than on foliage during the first generation.

Finally, success of chemical communication in insects may be enhanced by low wind speeds (Elkinton and Carde 1984). Partitioning mating and oviposition into different times of day may permit more efficient oviposition if females are allowed to proceed uninterrupted by males searching for calling females. The difference in mating periodicity between ABLM and STLM could serve as an isolating mechanism, as it does for other insects (Carde and Baker 1984, Haynes and Birch 1986), although the pheromones appear to be sufficiently different so as to preclude interspecific responses (Weires et al. 1980).

The difference in the time of day of mating intitiation between ABLM and STLM suggests a possible reason for their present geographical distribution. This distribution,

with ABLM located in generally warmer regions east and south of the Hudson River, and STLM west and north of this region, may be in part due to potentially increased mating success by STLM relative to ABLM in colder climates, as temperatures are typically warmer in the evening than in the morning. Cooler morning temperatures may prevent ABLM from mating, at least to a greater degree than evening temperatures would likely prevent STLM from mating.

## Conclusion

In this study, male ABLM were observed to take flight in early to mid-morning, possibly in response to pheromone calling by females. Mating occurred primarily on the undersides of leaves and from ca. 0700 through 1100 hours.

ABLM remained largely inactive from late morning to late afternoon, residing mostly on the lower third of the tree trunk during the first generation and on the undersides of leaves during the second and third generations. Oviposition activity began in late afternoon, and continued at least until sunset and darkness. During the first generation, oviposition was concentrated in the inner half of the tree canopy and below 1.5 m.

These observations suggest several strategies to optimize control of this pest, especially against the first generation. Pre-bloom insecticide application against ABLM adults is preferable to later season treatments (Green and Prokopy 1986). In brief, these reasons include the preservation of mite predators, which do not immigrate into apple trees until after bloom (Hislop and Prokopy 1981) and elimination of larval injury to foliage by controlling adults prior to oviposition. Larval injury to foliage may increase phytotoxic effects of nutrient and pesticide sprays, causing economic loss, especially in combination with stresses such as drought, mite infestation, and advanced tree age (Coli and Prokopy 1982, Reissig et al. 1982).

Prebloom insecticide treatments directed solely at the lower portion of the tree and ground cover may achieve effective control and provide a substantial savings in

insecticide cost. Adulticides applied during calm periods in late afternoon or early evening, when female ABLM are ovipositing or otherwise active, may maximize potential fumigant as well as direct-contact effects of insecticide. Good coverage of the interior of the tree canopy with spray material is particularly advisable.

A temperature/wind speed threshold may exist below which female ABLM will not engage in oviposition activity, as appears to be the case for temperature with STLM (Trimble 1986). Pre-bloom insecticide treatment could be delayed until conditions above threshold occur or are anticipated. Further work is needed to determine if such a threshold exists.

Table 1. Chronology of experiments and cumulative totals of observations of apple blotch leafminer (ABLM) adults (or larvae, experiment 6) conducted in (or adjacent to, experiment 3) commercial apple orchards in New England by generation.[a] Figures or tables in which results of experiments are presented are noted in parentheses.

| Experiment | Generation | Dates | Totals |
|---|---|---|---|
| 1. 1-min visual surveys of various apple tree structures for ABLM adults (Table 3) | 2 | July 8-10, 17-19, 1983 | 616 moths, 384 min |
| | 3 | Aug. 13-14, 1981 Aug. 16-18, 24, 26-27, 31, Sept. 7, 10, 1982 | 5148 moths, 1410 min |
| 2. Captures of adult ABLM observed in flight (Table 5) | 2 | July 8-9, 17-19, 1983 | 95 moths |
| | 3 | Aug. 18, 20, 24, 26-27, 31, Sept. 7-8, 1982 | 110 moths |
| 3. 1-min visual surveys of various non-host tree[b] structures for ABLM adults (Fig. 2) | 1 | May 17-18, 21-24, 26, 1984 | 7 moths, 102 min |
| | 2 | July 8-10, 17-19, 1983 June 30, July 14-15, 1984 | 101 moths, 366 min |
| | 3 | Aug. 14-15, 1984 | 39 moths, 78 min |
| 4. Activity of individual ABLM observed for 5-min periods (Fig. 1) | 1 | May 17-18, 21-24, 26, 1984 | 96 moths |
| | 2 | July 8-10, 17-19, 1983 June 30-July 1, 14-15, 1984 | 230 moths |

continued

Table 1. Continued

| | | | |
|---|---|---|---|
| 5. 1-min visual surveys of different areas of the tree canopy, trunk and ground cover (Table 2) | 1 | May 17-18, 21-24, 26, 1984 | 222 moths, 864 min |
| | 2 | June 30- July 1, July 14-15, 1984 | 992 moths, 944 min |
| | 3 | Aug. 14-15, 1984 | 2605 moths, 448 min |
| 6. Distribution of ABLM larval mines[c] (Table 4) | 1 | June 1, July 1, 1984 | 165 mines, 400 leaves, 8 trees |
| | 2 | July 29, Aug. 14, 1984 | 490 mines, 650 leaves, 13 trees |

[a] Locations: Aug. 13-14, 1981, Granville, MA; Aug. 16-18, 20, 24, 26-27, 31, Sept. 7-8, 10, 1982, Belchertown, MA; July 8-10, 17-19, 1983, Stratham, NH; May 17-26, June 30, July 1, 14-15, 1984, Shelburne, MA; Aug. 14-15 1984, Wilbraham, MA.

[b] Representative non-hosts were selected from trees within 20 m of apple trees and included maple, pine, oak, beech, poplar and sumac.

[c] First generation mines were sampled in Shelburne, and second generation mines were sampled in Wilbraham, MA.

Table 2. Diel periodicity of total ABLM and mating pairs observed during 1 minute visual surveys of undersides of apple leaves below 1.5 m in the inner half of the tree canopy (= LI), below 1.5 m height in the outer half of the canopy (= LO), between 1.5 m and 2.5 m height in the inner (= MI) and outer halves of the canopy (= LO), and within 1.5 m of the tree top (= TOP); on the tree trunk below 1.5 m height (= TKL), between 1.5 and 2.5 m height (= TKM), and within 1.5 m of the tree top (= TKT); in the ground cover outside of the tree dripline (= GCO), and under the outer (= GCM), and inner halves of the canopy (= GCI); and in flight (= FLT). Also given are concurrently measured weather parameters.[a]

| | | | | | | Average no. observed per minute[b] | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Individual moths | | | | | | | | | | | | Mating pairs | | | | |
| Gen. | Hour of day | Temp. (Co) | RH (%) | Wind speed (KPH) | Light intens. (lux) | LI | LO | MI | MO | TOP | TKL | TKM | TKT | GCO | GCM | GCI | FLT | LI | LO | MI | MO | TOP |
| 1 | 700 | 9 | 73 | 1.2 | 841 | 1.0 | 1.0 | 0.2 | 0.5 | 0.0 | 1.3 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 900 | 14 | 60 | 3.4 | 2705 | 1.0 | 0.7 | 0.9 | 0.6 | 0.1 | 1.0 | 0.1 | 0.0 | 0.0 | 0.1 | 0.1 | 0.4 | 0.0 | 0.1 | 0.0 | 0.3 | 0.0 |
| | 1100 | 19 | 41 | 5.5 | 5729 | 1.1 | 0.3 | 1.1 | 0.3 | 0.0 | 1.9 | 0.1 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1300 | 22 | 36 | 4.9 | 4313 | 0.4 | 0.4 | 0.1 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1500 | 23 | 34 | 5.8 | 5952 | 0.6 | 0.3 | 0.1 | 0.3 | 0.0 | 2.1 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1700 | 20 | 31 | 6.0 | 3914 | 0.8 | 0.5 | 0.6 | 0.1 | 0.1 | 0.8 | 0.3 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1900 | 20 | 38 | 5.4 | 643 | 0.0 | 1.0 | 1.5 | 1.5 | 0.0 | 1.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 2100 | 15 | 53 | 2.6 | 73 | 0.5 | 0.5 | 0.8 | 0.7 | 0.2 | 0.8 | 0.3 | 0.2 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | MEAN | 17.8 | 45.8 | 4.35 | 3021.2 | 0.68 | 0.59 | 0.66 | 0.50 | 0.05 | 1.30 | 0.16 | 0.04 | 0.01 | 0.01 | 0.04 | 0.05 | 0.00 | 0.01 | 0.00 | 0.04 | 0.00 |

continued

Table 2. continued

| Gen. | Hour of day | Temp. (Co) | RH (%) | Wind speed (KPH) | Light intens. (lux) | LI | Average no. observed per minute[b] Individual moths LO | MI | MO | TOP | TKL | TKM | TKT | GCO | GCM | GCI | FLT | Mating pairs LI | LO | MI | MO | TOP |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2 | 700 | 17 | 80 | 0.2 | 486 | 1.1 | 0.9 | 2.6 | 1.7 | 2.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.4 | 0.0 | 0.4 | 0.3 | 0.0 | 0.1 |
| | 900 | 21 | 63 | 0.6 | 2441 | 1.3 | 1.9 | 2.5 | 2.1 | 1.4 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 8.4 | 0.1 | 0.0 | 0.5 | 0.4 | 0.3 |
| | 1100 | 24 | 55 | 0.9 | 4584 | 1.4 | 2.0 | 4.6 | 2.8 | 3.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 | 0.8 | 0.3 | 0.1 |
| | 1300 | 26 | 49 | 3.1 | 6125 | 2.5 | 2.3 | 3.5 | 2.2 | 1.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.2 | 0.0 | 0.0 | 0.2 | 0.0 |
| | 1500 | 29 | 40 | 2.7 | 5664 | 3.7 | 2.0 | 4.5 | 3.0 | 2.8 | 0.3 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1700 | 27 | 43 | 2.1 | 3355 | 4.8 | 3.6 | 4.3 | 3.1 | 3.1 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1900 | 25 | 47 | 1.3 | 922 | 4.8 | 5.1 | 5.5 | 3.5 | 3.3 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 2100 | 22 | 56 | 0.5 | 283 | 4.0 | 2.5 | 3.4 | 1.5 | 1.6 | 0.1 | 0.0 | 0.4 | 0.0 | 0.0 | 0.1 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | MEAN | 23.9 | 54.1 | 1.43 | 2982.5 | 2.95 | 2.54 | 3.86 | 2.49 | 2.41 | 0.17 | 0.00 | 0.08 | 0.00 | 0.00 | 0.10 | 1.73 | 0.04 | 0.05 | 0.20 | 0.1 | 0.06 |
| 3 | 700 | 21 | 81 | 0.0 | 316 | 9.5 | 5.5 | 11.5 | 3.5 | 3.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 18.5 | 2.5 | 2.0 | 2.5 | 1.0 | 1.5 |
| | 900 | 22 | 72 | 0.2 | 1808 | 12.5 | 10.5 | 15.5 | 14.3 | 8.5 | 0.0 | 0.0 | 0.5 | 0.0 | 0.0 | 1.8 | 13.5 | 0.8 | 1.3 | 2.0 | 1.5 | 1.5 |
| | 1100 | 25 | 48 | 1.5 | 4375 | 18.8 | 11.5 | 17.8 | 10.5 | 9.3 | 2.5 | 2.5 | 0.8 | 0.0 | 0.0 | 1.3 | 0.0 | 0.3 | 0.3 | 0.3 | 0.5 | 0.3 |
| | 1300 | 28 | 44 | 2.3 | 4900 | 22.3 | 15.5 | 20.5 | 14.5 | 5.8 | 2.0 | 0.5 | 0.0 | 0.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1500 | 28 | 43 | 2.6 | 4576 | 20.8 | 14.8 | 21.5 | 12.3 | 5.0 | 5.3 | 0.5 | 0.3 | 0.0 | 0.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1700 | 28 | 42 | 2.4 | 3256 | 27.5 | 20.0 | 26.5 | 25.0 | 10.3 | 3.0 | 2.3 | 0.3 | 0.0 | 1.5 | 1.5 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1900 | 25 | 46 | 0.5 | 968 | 22.8 | 15.0 | 22.3 | 17.3 | 7.3 | 3.3 | 0.3 | 0.3 | 0.0 | 2.3 | 2.8 | 7.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 2100 | 22 | 61 | 1.0 | 41 | 2.5 | 8.5 | 13.0 | 10.0 | 6.0 | 0.0 | 0.5 | 0.5 | 0.0 | 2.5 | 2.5 | 49.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | MEAN | 24.9 | 54.6 | 1.31 | 2525.4 | 18.34 | 12.66 | 18.57 | 13.43 | 6.96 | 2.01 | 0.82 | 0.34 | 0.00 | 0.97 | 1.43 | 11.12 | 0.45 | 0.45 | 0.60 | 0.38 | 0.41 |

[a]Observations were conducted throughout the daylight hours over all three generations, 1984.

[b]Average N = 54, 59, and 28 min (generations 1-3, respectively) per location for each 2 hr. interval.

Table 3. Diel periodicity of ABLM adults and mating pairs observed during 1 minute visual surveys of leaf undersides (= LL), top sides of leaves (=UL), tree trunks (= TK), ground cover (= GC), fruit (= FRT), and in flight (= FLT), and concurrently measured weather parameters in commercial apple orchards throughout the daylight hours for the second and third generations 1981-83.

| | | | | | | Average no. observed per minute[a] | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Individual moths | | | | | | Mating pairs | | | | | |
| Gen. | Hour of Day | Temp. (C) | RH (%) | Wind speed (KPH) | Light intens. (lux) | LL | UL | TK | GC | FRT | FLT | LL | UL | TK | GC | FRT | FLT |
| 2 | 700 | 17 | 85 | 0.2 | 548 | 1.0 | 0.6 | 0.1 | 0.0 | 0.2 | 5.2 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 900 | 21 | 65 | 0.5 | 2659 | 2.9 | 0.5 | 0.5 | 0.2 | 0.1 | 12.9 | 1.1 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 |
| | 1100 | 24 | 57 | 0.7 | 5044 | 2.5 | 0.1 | 0.0 | 0.2 | 0.2 | 3.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 |
| | 1300 | 27 | 48 | 4.0 | 7967 | 8.0 | 0.0 | 1.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1500 | 28 | 46 | 2.0 | 7540 | 3.0 | 0.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1700 | 26 | 45 | 1.9 | 4404 | 3.5 | 0.0 | 0.7 | 0.7 | 0.2 | 0.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1900 | 24 | 48 | 1.4 | 1082 | 4.5 | 0.2 | 0.2 | 0.5 | 0.5 | 1.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 2100 | 21 | 55 | 0.6 | 413 | 3.7 | 0.3 | 0.4 | 0.0 | 0.2 | 6.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | MEAN | 23.5 | 56.1 | 1.42 | 3707.1 | 3.64 | 0.22 | 0.61 | 0.29 | 0.17 | 3.80 | 0.15 | 0.00 | 0.02 | 0.00 | 0.02 | 0.00 |
| 3 | 700 | 15 | 83 | 0.6 | 181 | 2.5 | 0.6 | 0.3 | 0.0 | 0.3 | 14.3 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 900 | 17 | 85 | 1.1 | 1417 | 3.2 | 1.1 | 0.7 | 0.3 | 0.3 | 39.8 | 0.4 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 |
| | 1100 | 24 | 59 | 1.3 | 3813 | 7.5 | 0.6 | 1.4 | 0.1 | 0.3 | 22.5 | 1.3 | 0.0 | 0.1 | 0.0 | 0.2 | 0.0 |
| | 1300 | 27 | 53 | 1.4 | 5038 | 11.0 | 0.7 | 4.0 | 0.0 | 0.1 | 1.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1500 | 26 | 50 | 0.7 | 5296 | 17.7 | 1.4 | 5.5 | 0.1 | 0.3 | 1.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1700 | 24 | 51 | 0.9 | 3912 | 12.5 | 0.4 | 3.2 | 0.2 | 0.1 | 1.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 1900 | 23 | 63 | 0.3 | 1177 | 7.3 | 1.1 | 2.4 | 0.4 | 0.4 | 12.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | 2100 | 19 | 81 | 0.0 | 44 | 3.9 | 1.8 | 1.1 | 0.1 | 0.6 | 13.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| | MEAN | 21.8 | 65.6 | 0.78 | 2609.8 | 8.21 | 0.97 | 2.33 | 0.16 | 0.31 | 13.40 | 0.22 | 0.00 | 0.02 | 0.00 | 0.03 | 0.00 |

[a]Average N = 64 (second generation) and 235 (third generation) min per location for each 2-h interval.

Table 4. Distribution of ABLM adults on the undersides of apple leaves determined by 1-min visual surveys, and of larval mines per leaf in 5 areas of the tree canopy, during the first and second generations in commercial apple orchards, 1984.

| Tree Area | | Percentage[a] ± SE First Generation | Second Generation[b] |
|---|---|---|---|
| Inner half of canopy, below 1.5 m height | Moths | 31.9 ± 0.4% | 20.6 ± 0.1% |
| | Mines | 35.6 ± 0.3 | 27.8 ± 0.1 |
| Inner half of canopy, between 1.5 and 2.5 m height | Moths | 25.2 ± 0.4 | 27.0 ± 0.1 |
| | Mines | 23.6 ± 0.3 | 23.5 ± 0.1 |
| Outer half of canopy, below 1.5 m height | Moths | 23.5 ± 0.4 | 18.1 ± 0.1 |
| | Mines | 20.0 ± 0.3 | 14.7 ± 0.1 |
| Outer half of canopy, between 1.5 and 2.5 m height | Moths | 16.8 ± 0.3 | 17.4 ± 0.0 |
| | Mines | 13.3 ± 0.2 | 15.1 ± 0.1 |
| Within 0.5 m of tree top | Moths | 2.5 ± 0.1 | 17.0 ± 0.0 |
| | Mines | 7.3 ± 0.2 | 18.9 ± 0.1 |

[a] Of all moths or mines observed, percentage observed in each tree area, within a generation. Total observation times for moths were 270 and 295 min, with 0.44 and 2.87 moths observed per min for the first and second generations respectively. Eight and 13 trees were sampled for first and second generation mines, respectively, and 10 leaves were sampled per tree area in each tree. Overall mines were 0.41 and 0.75 per leaf for first and second generations, respectively.

[b] Due to an insecticide application applied against ABLM larvae of the second generation, larval mines were sampled in a different orchard.

Table 5. Of total adult ABLM captured, proportion (± S. E.) that were males. ABLM were captured in flight by sweep net or immediately post-flight by aspiration from 0500 to 1000 hours and from 1600 to 2100 hours in commercial apple orchards.[a]

| | Total Captures | Proportion of Males in Total Captures | |
|---|---|---|---|
| | | 0500-1000 hours | 1600-2100 hours |
| Aspiration | 60 | 0.92 ± 0.02 | 0.19 ± 0.01 |
| Sweep Net | 145 | 0.98 ± 0.00 | 0.05 ± 0.01 |

[a] Captures were made on 5 days of the second generation (July 8, 9, 17-19, 1982) and 8 days of the third generation (Aug. 18, 20, 24, 26, 27, 31 and Sept. 7, 8, 1981).

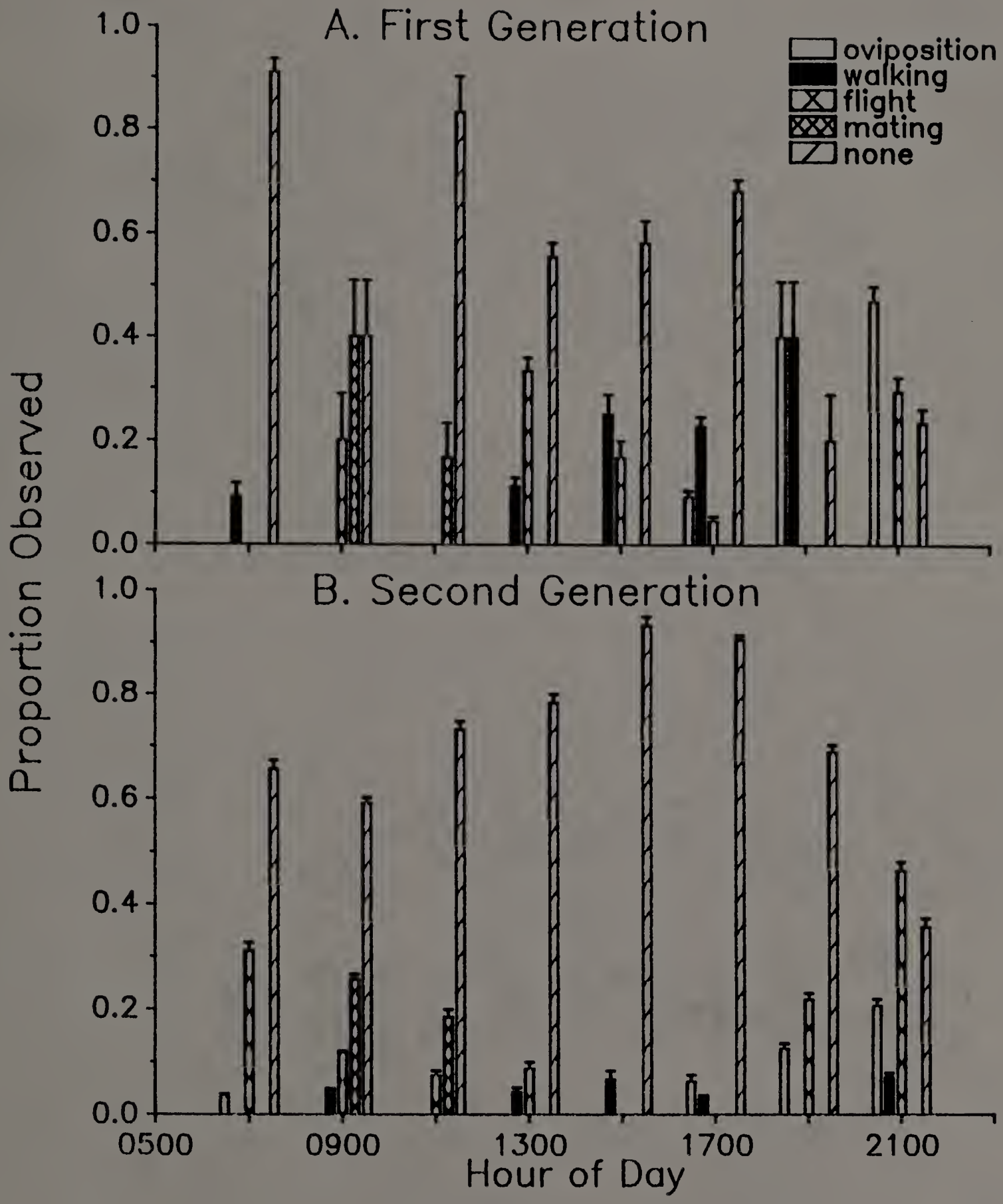



Figure 1. Diel periodicity of activity of ABLM individuals observed for 5-min periods throughout the day during the first (A) and second (B) generations on apple trees in commercial orchards, 1983-84. Data given as ± S. E. Each individual observed was categorized as ovipositing (probing lower leaf surface with the ovipositor or depositing an egg), walking only, walking and flying or flying only (= flight), mating, or stationary (= none). Total N values are 96 and 230 moths for first and second generations respectively.

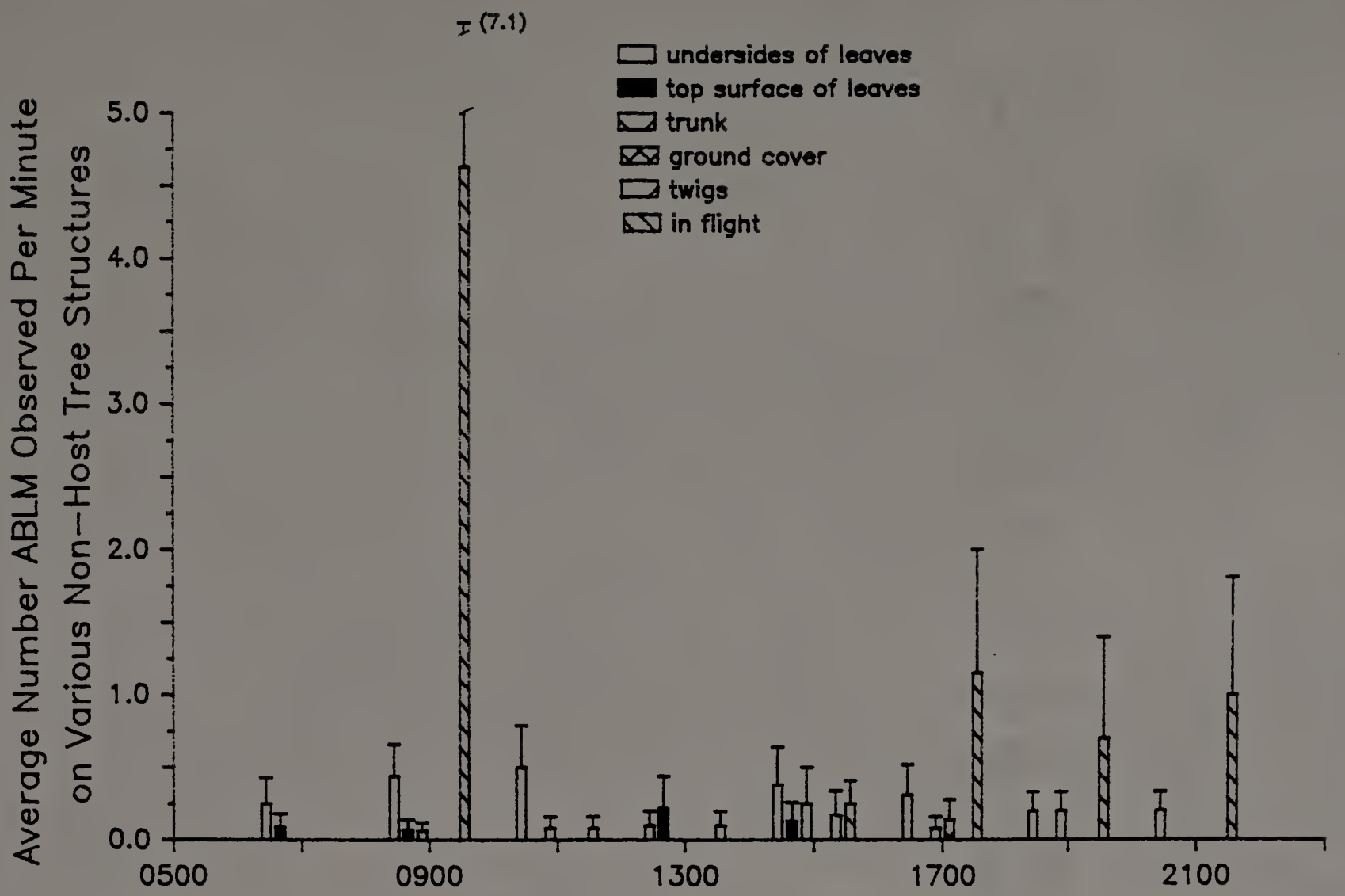



Figure 2. Diel periodicity in total number of ABLM adults observed per min by visual survey of leaf undersides, tree trunk, ground cover, twigs, and top sides of leaves, and of the tree canopy for ABLM in flight on non-host trees within 20 m of commercial apple orchards throughout daylight hours for all three generations, 1983-84. Average N = 91 min per location for each 2-h interval. All data are given as ± S. E.

# CHAPTER 2

## OVIPOSITION BEHAVIOR OF THE APPLE BLOTCH LEAFMINER, *PHYLLONORYCTER CRATAEGELLA* (CLEMENS) (LEPIDOPTERA: GRACILLARIIDAE)


Abstract

Observations of oviposition by apple blotch leafminer moths, *Phyllonorycter crataegella* (Clemens), on apple foliage in the field and in the laboratory indicated oviposition occurred solely on the undersides of leaves, and primarily on the middle third of the leaf (between petiole and apical tip), midway between the mid-vein and margin. A stereotypical sequence of events lasting ca. 1 min was observed prior to egg deposition. This included walking while tapping the leaf underside with the antennae, probing a small area (ca. 1 cm2) of the leaf with the ovipositor, and violent side-to-side shaking of the abdomen at egg deposition. Results of choice tests in the laboratory suggest apple blotch leafminer moths do not discriminate against oviposition sites previously occupied by freshly deposited conspecific eggs.


Introduction

The apple blotch leafminer, *Phyllonorycter crataegella* (Clemens) (ABLM), is one of several gracillariid species infesting apple in North America. The ABLM is found in the Hudson River Valley, east of that throughout much of New England, and south to Virginia (Beckham et al. 1950, Weires et al. 1980, Coli and Prokopy 1982, Maier 1983, Van Driesche and Taub 1983). It parasitizes at least 17 host plants in 7 genera in New England (Maier 1985). ABLM has achieved major pest status in commercial apple

orchards in New York and New England over the past 13 years due to its development of resistance to organophosphate insecticides (Weires 1977, Weires et al. 1982, Van Driesche et al. 1985).

The ABLM completes three generations per year, with the first adults emerging in early spring from pupae in the previous season's leaves. Female ABLM deposit eggs singly on the undersides of host leaves from mid- to late afternoon until sundown (Green and Prokopy 1984, Chapter I). Adult ABLM and larval mines are concentrated in the lower part of apple tree canopies in commercial orchards during the first generation, spreading upwards in succeeding generations (Beckham et al. 1950, Green at al. 1985, Chapter I). The oviposition behavior of this insect may have important implications for management programs directed against this pest (Green et al. 1985, Chapter I).

Competition for resources could be more important for leafmining insects than for species that are more mobile in larval stages, as leafminers typically spend their entire larval life within one leaf or portion of a leaf (Bultman and Faeth 1985). Intraspecific competition has been demonstrated for other leafmining insects (Parella 1983, Quiring and McNeil 1984, Potter 1985), including gracillariid species (Martin 1956, Bultman and Faeth 1986).

Where competition is important, evolution may favor the development of mechanisms allowing individuals to detect and avoid resources already occupied by conspecifics (Prokopy 1972, McNeil and Quiring 1983, Prokopy et al. 1984). Some of these mechanisms may have potential as pest management tools (Prokopy 1981, Roitberg and Prokopy 1987).

The objectives of the following study were to examine and describe the oviposition behavior of female ABLM in detail, and to examine possible discrimination against host leaves previously occupied by conspecific eggs.

Materials and Methods

All observations of ABLM oviposition in the field (experiment 1) were conducted in commercial apple orchards in New England during 1983 and 1984, as part of a larger study of ABLM behavior (Chapter I). An area within the canopy of an apple tree was selected at random, and the undersides of leaves were searched until an ABLM adult was located. The activity of the moth was recorded for 5 min, or until the moth flew out of sight of the observer. If oviposition activity was observed, the number of ovipositions, leaves visited, repeat visits to the same leaf, and leaves receiving eggs were recorded and are reported here. Also recorded was whether a moth arrived on a leaf by flight or by walking.

ABLM observed in the laboratory (experiments 2, 3, 4) were collected as pupae in leaves from commercial apple orchards in western Massachusetts. The portions of leaves containing mines were held individually in 30 ml plastic cups until adult emergence. Upon emergence, ABLM were placed collectively in a 3.8 l glass jar, the opening of which was covered with organdy cloth to permit air circulation. Each morning, mating pairs were removed from the jar and placed in the cups until females were used for experimentation the following day. Throughout, ABLM adults were provided free access to spring water-soaked dental wicks, and maintained under natural lighting in front of a large screened window. All laboratory experiments, conducted on a table placed in front of this window, occurred from 1500-2100 hours (DST), the time of peak ABLM oviposition in the field (Chapter I).

Foliage used in laboratory experiments was collected daily from unsprayed apple trees and carefully examined to exclude leaves with leafminer eggs or larval mines. Only basal leaves (or fruit cluster leaves, experiment 4) of growing terminals were selected for use in the choice tests to provide uniform leaf age and quality. Leaves were maintained on the terminals, which were held in water-filled vials. Average leaf size in experiments 2 and 3 was 6.2 by 4.2 cm.

During the summer of 1984, 23 ABLM were observed individually in the laboratory for 3 h each (experiment 2). Each moth was held in a vertical cylindrical cage of clear acetate (14 cm diameter, 25 cm height), containing an apple terminal with 8 leaves. The base of the terminal extended through a hole in the floor of the cage (a plastic petri dish bottom) and into a vial containing water to prevent wilting. The top of the cage was covered with organdy cloth to allow air circulation.

ABLM females were placed singly in a stoppered vial within the cage, and were allowed to acclimate for 5 min before the cotton stopper was removed (remotely, by pulling a string) and observations were begun. The number and sequence of leaf visits, number and location of ovipositions, and the sequence of behaviors involved in oviposition were timed and recorded.

After the 3-h period expired, the moth was removed from the cage. The number of ovipositions was confirmed by examination of leaves under a microscope, and the length and width of each leaf was measured and recorded. The location of the first egg only (to eliminate any influence of previous ovipositions) on each leaf was plotted according to distance from petiole, margin, and midrib.

In the third experiment, conducted during the summer months of 1984, individual ABLM females (caged as in experiment 2) were provided with a terminal of 2 leaves, one containing 1 or 8 ABLM eggs (oviposited < 30 h previously) and one without prior ovipositions (= clean). Each female was observed 30 min or until the first oviposition. Each female was pre-tested by being allowed to oviposit freely on a clean leaf until it left the leaf. Only females which oviposited at least once in the pretest were used in the experiment.

In a final experiment, conducted in July of 1987, individually caged ABLM females were provided with 2 small leaves (average size 2.3 by 1.4 cm), one clean and one with 1 or 2 prior ovipositions. The leaf half (right or left of the midvein) containing or receiving eggs was noted. ABLM females were pre-tested by being offered 3 pairs of

leaves in succession, the next pair being offered after one oviposition. Only females which oviposited three times prior to the assay were used.

Results

In commercial apple orchards, 25 ABLM females were observed exhibiting oviposition behaviors (Table 6), all between 1645 and 2035 hours. Of the 25, 8 moths were observed probing the leaf underside with the ovipositor but did not oviposit while under observation. All ovipositions occurred on the undersides of leaves, though arrival was on the upper surface of leaves in about half of all visits. Overall, 19.1% of leaves visited received an egg, and 8.8% of all leaf visits were repeat visits by the same female to the same leaf. No moths oviposited more than once per leaf visit. In one instance a second egg was placed on a leaf previously oviposited on by the same female during a prior visit. About two-thirds of leaf visits were via walking from the stem or adjacent leaves (Table 6). About one-third were by flight.

Of the 23 moths observed in the laboratory for 3 h, 19 visited foliage and 15 oviposited at least once, for an overall average of 6.7 eggs per female (range = 0-20, Table 7). After tarsal contact with a leaf, females spent an average of 30 s walking on the leaf, during which they continuously tapped the leaf surface with the antennae, gradually narrowing down the area "searched" by walking in an increasingly tighter circle. Once ovipositor contact with the leaf occurred, females spent an average of 29 s probing a small area of the leaf (ca. < 1 cm2) with the ovipositor, often taking short, backward steps. This period ended with the abdomen bent at a near 90o angle to the rest of the body and the ovipositor firmly planted against the underside of the leaf. The female then shook violently 3-5 times from side to side, for a total of about 1 s, after which time the egg was deposited on the leaf surface. The moth then quickly lifted the abdomen and ovipositor off the leaf surface, and crawled away from the egg.

On the first leaf visit by laboratory-observed moths, females frequently oviposited more than once before leaving (mean 1.7 eggs/first leaf visit/female). They did so much less frequently on subsequent leaf visits (mean 0.7 eggs/leaf visit/female). Among the 15 replicates where oviposition occurred, 78% of leaf visits did not result in an oviposition.

Females oviposited preferentially on the middle of three lateral sections the leaf (sectioned perpendicular to mid-vein, Fig. 3A), and the middle second and third quarters longitudinally (sectioned parallel to mid-vein, Fig. 3B). No preference was exhibited for any particular leaf position within a terminal relative to the most basal or apical leaf (Table 8).

In the choice tests, no significant differences were detected in the number of new ovipositions on clean leaves vs. leaves with one or eight prior ovipositions, although substantially more new eggs were placed on clean leaves vs. leaves with 8 prior ovipositions (Table 9).

In choice tests using small leaves, leaves with one prior oviposition received new eggs as often as did clean leaves (Table 10). Of the 14 new eggs placed on leaves with a prior oviposition, 7 were placed on the same half (right or left side of the mid-vein) of the leaf underside as the initial egg. Leaves with 2 prior ovipositions received new eggs significantly more times than did clean leaves. Overall, the first leaf visited received the first oviposition in 23 of a total of 41 ovipositions.

## Discussion

Repeated attempts to encourage ABLM females to oviposit while being observed in the laboratory under artificial lighting were unsuccessful. Females confined for several days with foliage under those conditions did oviposit eventually. Success in gaining oviposition within a limited time was attained when ABLM were maintained and offered

foliage in front of a screened window, under natural lighting, temperature, and humidity, and during the time period within which oviposition occurs in the field.

Results of this study agree with observations by Beckham et al. (1950) of a concentration of oviposition by ABLM on the mid-section of the leaf. Pottinger and LeRoux (1971) found no preference for the proximal or distal leaf half by a related species, the spotted tentiform leafminer (STLM), Phyllonorycter blancardella (F.), but they did not report distribution by thirds as presented here. They described a sequence of behaviors during oviposition by STLM similar to that of ABLM described here, including antennal tapping of leaves, and violent shaking immediately prior to egg deposition. They hypothesized the shaking served to clear the leaf surface and/or ready the egg for deposition. They recorded a remarkably similar mean time from ovipositor contact with the leaf to egg deposition (27.3 s vs. 29.4 s here), and also observed many leaf visits without oviposition. They observed one instance of multiple oviposition (2 eggs) by the same female during the same visit to a single leaf in the field.

ABLM mate at temperatures at least as low as 7o C (Chapter I), but oviposition may be restricted to periods of higher temperature (> 9-15o C) and low wind speeds (Trimble 1986, Chapter I). Therefore, the potential may exist for a considerable buildup of mated female ABLM in sheltered locations until conditions are right for oviposition. Once these conditions occur, ABLM females are capable of ovipositing up to 20 eggs each (average = 6.7 eggs per female) during a single 3-h period. Thus, when needed, orchardists should apply adulticides against ABLM just prior to or during the first warm (> 9-12 o C), calm evening in the spring when foliage and ABLM adults are present.

A topic of considerable interest in the recent literature has been the extent and importance of inter- and intraspecific competition in regulating natural populations (Lawton and Strong 1981, Schoener 1982, 1983). Intraspecific competition for larval resources may not occur in populations maintained at low densities by natural enemies

(Faeth and Simberloff 1981). Regulation of ABLM population densities by parasites has been noted by many workers (Dean 1940, Gambino and Sullivan 1982, Maier 1982, Van Driesche and Taub 1983, Van Driesche et al. 1985, Drummond et al. 1985). However, a number of factors may enhance the possibility of competition among ABLM, even at low ABLM densities, by limiting the availability of superior leaves or portions of leaves as larval resources.

As in most but not all lepidopteran leafminers (Gross 1986), the ABLM larva is restricted to one area of a leaf (larvae do not cross major leaf veins) for its entire larval life. The parent female chooses that site. This could tend to favor natural selection for females capable of choosing a favorable site if resources are not homogeneous.

Results of this study indicate ABLM females oviposit preferentially on the mid-section of leaves, suggesting some favorable quality about this portion of the leaf. Also, females concentrate oviposition within the interior half of the tree canopy throughout the season, and in the lower portion of the canopy during the first generation (Beckham et al. 1950, Chapter I). This part of the canopy may be preferred due to less wind interference with oviposition (Chapter I), closer proximity to emergence sites (Beckham et al. 1950), or a reduced tendency for interior leaves to abscise prior to completion of larval development (Bultman and Faeth 1986b).

Additional factors may tend to limit availability of favorable oviposition sites, including the lesser amount of foliage in the spring and proximity to shelter (Martin 1956). Selection of leaves by leafminers by leaf size (Bultman and Faeth 1986a), nutrient content, or exposure to the sun (Faeth et al. 1981), or selection against leaf noxious compounds or damaged leaves (Faeth 1985) may also occur. The "choosiness" of ABLM noted here (i.e. visiting many leaves without ovipositing, Table 6), suggests that these or other factors may operate in ABLM oviposition site selection.

Restricted availability of superior oviposition sites may lead to over-utilization of exisiting sites. Interference competition among larvae, including cannibalism, has been

demonstrated in other gracillariids, including STLM (Pottinger and LeRoux 1971) and the aspen blotch leafminer, *Phyllonorycter salicifoliella* (Chambers) (Martin 1956), and in the dipteran leafminers *Agromyza frontella* (Rondani) (Quiring and McNeil 1983) and Liriomyza trifolii (Burgess) (Parrella 1983). Interference competition without cannibalism has been observed in another dipteran, the native holly leafminer, *Phytomyza ilicicola* Loew (Potter 1985). Besides cannibalism, the presence of conspecifics may also result in a general depletion of resources, or in induction of plant defenses.

Restricted availability of favorable oviposition sites suggested in this study and limited mobility of ABLM larvae are ecological characteristics which have been positively correlated with host marking ability (Prokopy 1981, Roitberg and Prokopy 1982, 1987). Host marking provides information about conspecific density. This information can then be used to avoid reduced fitness or mortality due to overcrowding. Additional positive corellates confirmed for ABLM include limited moth mobility (Beckham 1950, Green and Prokopy 1986) and relatively permanent host plants (present over 3 generations). The broad host range of ABLM (17 species, Maier 1985) is one characteristic not generally found in species which mark hosts. Given the concentrated searching behavior by ABLM prior to oviposition and the presence of ABLM eggs on the surface of the leaf, host marking may not be required for ABLM to recognize previously occupied sites.

The observation of at least one ABLM female ovipositing more than once on the same leaf in the field (experiment 1), the lack of discrimination by ABLM females against leaves with one egg (experiment 3), the concentrated "searching" behavior over a small leaf area prior to oviposition in the lab (experiment 2) and the ability of a single apple leaf to support several ABLM larvae suggest that the biologically significant unit chosen for egglaying by a female may be a portion of the leaf rather than the entire leaf. The substantially though not significantly greater new oviposition on clean leaves vs. leaves

with 8 prior ovipositions (Table 9) suggested possible discrimination on the basis of prior egg density. However, in all but 2 of the replicates, the first leaf visited received the first oviposition. Any discrimination against the leaves with 8 prior ovipositions would have been on the basis of cues other than contact with the leaf or eggs.

In experiment 3, ABLM females oviposited on the first leaf visited (53 of 55 replicates, or 96%), regardless of the presence or absence of prior ovipositions. For some unknown reason, ABLM females were not nearly as selective as they were in the field or in experiment 2, where only 19% and 32% of leaf visits resulted in oviposition, respectively. The discrepancy in moth selectivity calls into question the validity of this assay for determining discrimination by ABLM females.

Resolving these concerns was the rationale for the final experiment, in which small leaves were used and the leaf-half receiving the new egg was noted (Table 10). By restricting the amount of leaf area available and comparing oviposition on the basis of a portion of the leaf, any discrimination by females against small occupied areas of the leaf might become apparent. Pretesting each female on 3 clean leaves (vs. only 1 in experiment 3) was intended to accentuate "choosiness" by reducing any effect of oviposition deprivation and by providing uniform pre-assay oviposition experience which could be necessary for recognition of conspecific eggs or host markers.

"Choosiness" was greater in this experiment (56% of leaf visits resulted in an oviposition) than in experiment 3, but still not equal to levels observed in orchards or in experiment 2. No discrimination was detected against entire leaves or leaf halves containing one or two previous ovipositions. On the contrary, significantly more leaves with 2 prior ovipositions received new eggs than did clean leaves. This strongly suggests that some other factors, possibly related to leaf quality per se, are more important in ABLM selection of leaves for egglaying than the presence of conspecific eggs.

The apparent failure of ABLM females to discriminate against previously egg-occupied host leaves or parts of host leaves here could be due to reduced "choosiness" of

ABLM in this study. Alternatively, ABLM females may discriminate only at egg densities greater than those tested here or only against sites occupied by eggs that are more mature or against sites occupied by larvae.

Another hypothesis is that a conspecific egg recognition/ discrimination system may not have developed in ABLM because of insufficient selection pressure for such a system. Natural enemy regulation of ABLM populations, the broad host range of ABLM, and the capacity of a single leaf to support several ABLM larvae (Reissig et al. 1982) may act to reduce the intensity and/or frequency of intraspecific competition. The costs associated with maintaining such a system, including energetic costs and potential costs due to use of host marking cues by natural enemies may outweigh any benefits (Roitberg and Prokopy 1987).

Conclusion

Female ABLM exhibit considerable "choosiness" in selecting oviposition sites in commercial orchards and to a lesser extent in the laboratory. This selectivity includes a concentration of oviposition in the interior and lower portion of the tree canopy, preference for the middle portion of the leaf, extensive (avg. 30 s) examination of leaves prior to oviposition, and apparent rejection of ca. 80% of leaves visited in the field. ABLM females did not show significant discrimination against large leaves containing 8 prior conspecific ovipositions, nor against large or small leaves or small leaf-halves with 1 or 2 previous ovipositions.

Females followed a fairly stereotyped sequence of behaviors during oviposition in the lab, continuously tapping the leaf with the antennae, searching a progressively smaller area, probing the leaf underside with the ovipositor, and shaking violently from side to side before depositing an egg.

Aspects needing additional work include examination of the distribution of ABLM eggs and larvae in the field for clumped, random or uniform dispersion, density dependent

effects on larvae occurring from presence of conspecifics on the same leaf or different leaves on the same tree, and possible discrimination by ovipositing adults against leaves or portions of leaves occupied by conspecific eggs that are more mature or by larvae.

Table 6. Observations of ABLM exhibiting oviposition behavior (= ovipositor in contact with leaf) in commercial apple orchards in New England, 1983-1984.[a]

| | Mean Per Moth (± S. E.) |
|---|---|
| Minutes observed | 3.7 ± 0.69 |
| Number leaf visits | 4.1 ± 0.52 |
| Number different leaves visited | 3.8 ± 0.47 |
| Number ovipositions observed | 0.8 ± 0.62 |
| | Proportion ± S. E. |
| Proportion leaves visited | |
| by walking | 69.6 ± 0.01 |
| by flight | 30.4 ± 0.01 |

[a] Twenty-five moths were observed individually for 5 min or until leaving sight of observer. Data include 9, 12 and 4 ABLM during first through third generations, respectively.

Table 7. Sequence and duration of oviposition behaviors of individually caged ABLM females (48-72 h post-eclosion, 24-48 h post-mating) provided with apple terminals bearing 8 leaves and observed for 3 h.[a]

| Behavior | Duration (s) ± S. E.[b] |
|---|---|
| Tarsal contact with leaf | |
| until | 30.0 ± 3.08 |
| ovipositor contact with leaf | |
| until | 29.4 ± 3.40 |
| egg deposition initiation | |
| until | 13.1 ± 1.01 |
| crawl away from egg | |

[a] Total replicates = 23 moths (69 h of observation); 19 moths visited foliage; 15 moths oviposited at least once.

[b] Total N = 154 ovipositions; average eggs/female = 6.7 (range = 0-20).

Table 8. Distribution of eggs oviposited by individually caged ABLM females provided with a terminal of 8 apple leaves for 3 h.[a]

| Leaf Location on Terminal | Mean No. Eggs Per Leaf ± S. E.[b] |
|---|---|
| 1 (most basal) | 1.8 ± 0.11 |
| 2 | 0.9 ± 0.06 |
| 3 | 1.2 ± 0.08 |
| 4 | 1.3 ± 0.08 |
| 5 | 1.2 ± 0.08 |
| 6 | 1.5 ± 0.09 |
| 7 | 1.3 ± 0.08 |
| 8 (apical) | 0.6 ± 0.04 |

[a]Data reported are from 15 replicates in experiment 2 where oviposition occurred.

[b]Among 8 leaves, number of eggs deposited per leaf not significantly different ($P > 0.05$, ANOVA, Sokal and Rohlf 1981).

Table 9. Comparison of oviposition by individually caged ABLM females provided with two leaves, one free of conspecific eggs (= clean), the other with 1 or 8 ABLM eggs deposited < 30 h previously.

| | | Leaf Receiving New Egg[a] | |
|---|---|---|---|
| Treatment | N | Treated | Clean |
| 1 previous egg | 26 | 14 | 12 |
| 8 previous eggs | 29 | 10 | 19 |

[a] ABLM were allowed unlimited oviposition on a single clean leaf < 15 mins. prior to testing. Number of new ovipositions on clean vs. treated leaves not significantly different (P > 0.05, G-test, Sokal and Rohlf 1981).

Table 10. Comparison of oviposition by individually caged ABLM females provided with 2 leaves, one free of conspecific eggs (= clean) and one with 1 or 2 ABLM eggs deposited < 30 h previously. Of leaves with prior oviposition, comparison between halves of leaves (leaf divided by the midvein) receiving the new egg.

| | | Leaf Receiving New Egg[a] | |
|---|---|---|---|
| Treatment | N | Treated | Clean |
| 1 previous egg | 28 | 14a | 14a |
| 2 previous eggs | 13 | 11a | 2b |
| | | Leaf Half Receiving New Egg | |
| | | Treated Half | Clean Half |
| 1 previous egg | 14 | 7a | 7a |
| 2 previous eggs | 7 | 5a | 2a |

[a] First egg on leaf only, ABLM were allowed a single oviposition on each of 3 clean leaves < 30 mins. prior to testing. Means within a row and followed by the same letter are not significantly different (P > 0.05, G-test, Sokal and Rohlf 1981).

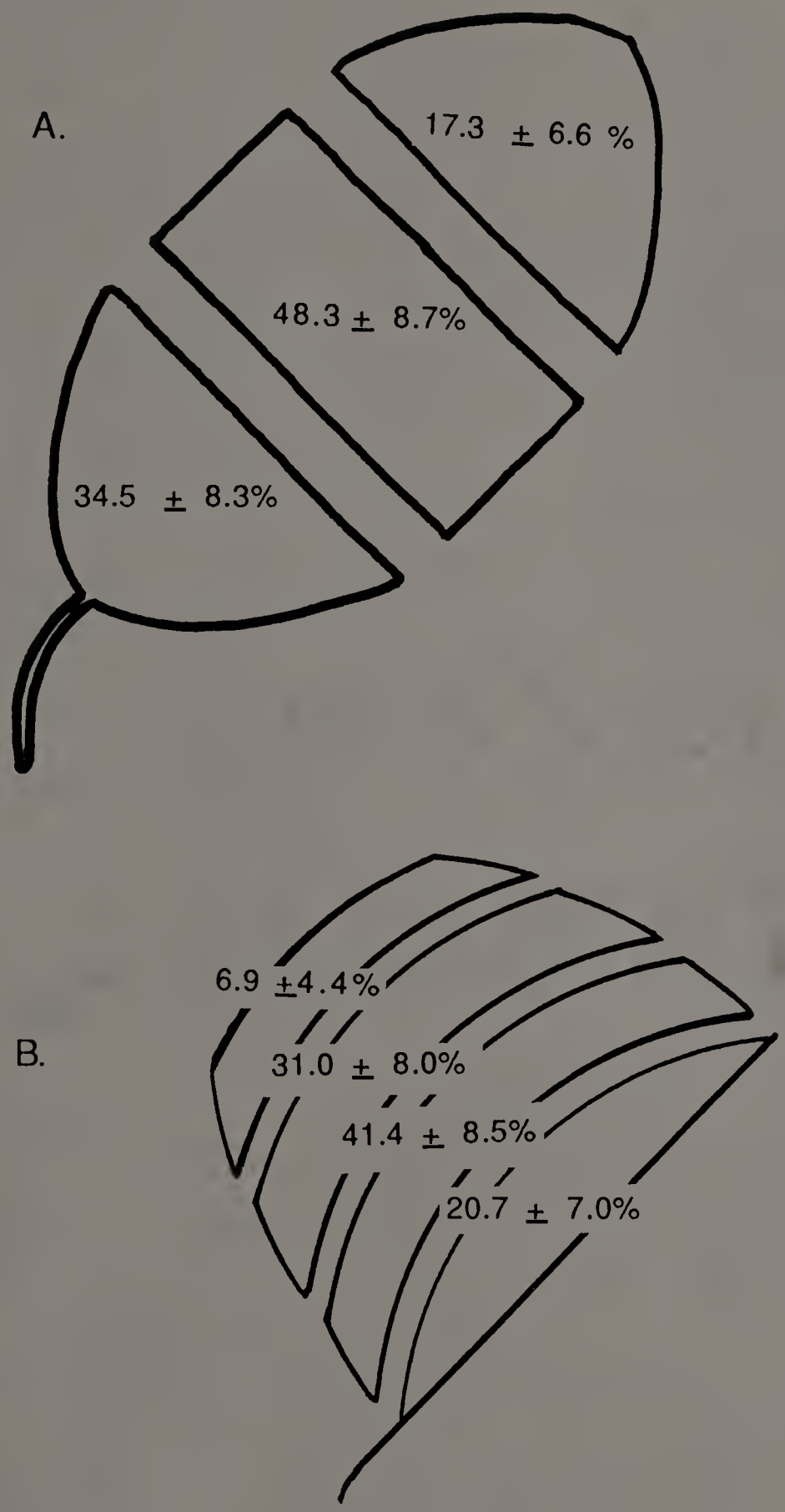



Fig. 3. Lateral (a) and longitudinal (b) distribution of ABLM eggs according to leaf surface area ± S. E. Eggs deposited during 3 h observations in laboratory. Only the first egg deposited on any leaf was included, N = 58 eggs, 15 moths.

## BIBLIOGRAPHY


Alm, S. R., R. W. Weires, R. C. Lamb, R. A. Nielsen, and J. R. VanKirk. 1985. Susceptibility of Malus spp. to the apple blotch leafminer (Lepidoptera: Gracillariidae). Environ. Entomol. 14: 228-230.

Askew, R. R., and M. R. Shaw. 1979. Mortality factors affecting the leaf-mining stages of Phyllonorycter (Lepidoptera: Gracillariidae) on oak and birch. 2. Biology of the parasite species. Zool. J. Linn. Soc. 67: 51-64.

Barrett, B. A., and C. D. Jorgensen. 1986. Parasitoids of the western tentiform leafminer, *Phyllonorycter elmaella* (Lepidoptera: Gracillariidae), in Utah apple orchards. Environ. Entomol. 15: 635-641.

Beckham, C. M., W. S. Hough, and C. H. Hill. 1950. Biology and control of the spotted tentiform leaf miner on apple trees. Va. Agric. Exp. Stn. Tech. Bull. 114: 1-19.

Bradley, J. B., S. N. A. Jacobs, and W. G. Tremewan. 1969. A key to the British and French species of Phyllonorycter Hubner (Lithocolletis Hubner) (Lepidoptera: Gracillariidae) (adapted from le Marchand, 1936). Entomol. Gaz. 20: 3-33.

Braun, A. F. 1908. Revision of the North American species of the genus Lithocolletis Hubner. Trans. Amer. Entomol. Soc. Phil. 34: 269-357.

Brunn, A. E. 1883. Tineidae infesting apple trees at Ithaca. Cornell Univ. Exp. Stn., 2nd Rpt., pp. 148-151.

Bultman, T. L. and S. H. Faeth. 1985. Patterns of intra- and interspecific association in leaf-mining insects on three oak host species. Ecol. Entomol. 10: 121-129.

1986. Experimental evidence for intraspecific competition in a lepidopteran leaf miner. Ecology 67 (2): 442-448.

1986a. Leaf size selection by leaf-mining insects on *Quercus emoryi* (Fagaceae). Oikos 46: 311-316.

1986b. Selective oviposition by a leaf miner in response to temporal variation in abscission. Oecologia 69: 117-120.

Carde, R. T., and T. C. Baker. 1984. Sexual communication with pheromones. In Chemical Ecology of Insects. W. T. Bell and R. T. Carde, eds. Chapman and Hall Ltd. Pp. 355-383.

Clemens, B. 1859. Contributions to American Lepidopterology - No. 2. Proc. Acad. Natl. Sci. Phil. XI: 324.

1861. Contributions to American Lepidopterology - No. 5. Proc. Acad. Natl. Sci. Phil. XII: 208.

Cochran, W. G. 1977. Sampling Techniques. 3rd ed, Wiley & Sons, N. Y. 428 pp.

Coli, W. M., and R. J. Prokopy. 1982. Biology, monitoring and control of leafminers in Massachusetts. Proc. Mass. Fruit Growers' Assoc. Annu. Mtg. 86: 30-44.

Coli, W. M., R. Zahnleuter, D. Gordon, K. Leahy, J. Parella, D. Roberts, and R. J. Prokopy. 1983. Integrated management of apple pests in Massachusetts, 1982 results: Insects. Mass. Fruit Notes 48 (1): 24-34.

Coli, W. M., T. A. Green, T. A. Hosmer, and R. J. Prokopy. 1985. Use of visual traps for monitoring insect pests in the Massachusetts apple IPM program. Agric. Ecosys. & Environ. 14: 251-265.

Common, F. B. 1975. Evolution and classification of the Lepidoptera. Annu. Rev. Entomol. 20: 183-203.

Dean, R. W. 1940. Spotted tentiform leafminer. Proc. N. Y. State Hortic. Soc. 89: 192-193.

1963. Control of tarnished plant bug and leafminers. Proc. N. Y. State Hortic. Soc. 103: 201-205.

Dixon, W. J., ed. 1983. BMDP Statistical Software. Univ. of Calif. Press, Berkeley, Calif. 734 pp.

Doganlar, M., and A. Mutuura. 1980. A new species of Phyllonorycter Hbn. (=Lithocolletis Hbn.) (Lepidoptera: Gracillariidae) from western North America. Can. Entomol. 112: 311-314.

Drummond, F. A., R. G. Van Driesche, and P. A. Logan. Model for temperature-dependent emergence of overwintering *Phyllonorycter crataegella* (Clemens) (Lepidoptera: Gracillariidae), and its parasitoid *Sympiesis marylandensis* Girault (Hymenoptera: Eulophidae). Environ. Entomol. 14: 305-311.

Dutcher, J. D., and A. J. Howitt. 1978. Bionomics and control of *Lithocolletis blancardella* in Michigan. J. Econ. Entomol. 71: 736-738.

Elkinton, J. S., and R. T. Carde. 1984. Odor dispersion. In Chemical Ecology of Insects. W. T. Bell and R. T. Carde, eds. Chapman and Hall Ltd. Pp. 74-91.

Fabricius, J. C. 1781. Exhibentes eorum differentias specificas, synonyma auctorum, loca natalia, metamorphosin adeictis observationibus descriptionibus. Species insectorum 2:305.

Faeth, S. H. 1985. Host leaf selection by leaf miners: interactions among three trophic levels. Ecology 66 (3): 870-875.

Faeth, S. H., and D. Simberloff. 1981. Population regulation of a leaf-mining insect, Cameraria sp. nov., at increased field densities. Ecol. 62(3): 620-624.

Faeth, S. H., S. Mopper, and D. S. Simberloff. 1981. Abundances and diversity of leaf-mining insects on three oak host species: effects of phenology and nitrogen content of leaves. Oikos. 37: 238-251.

Gambino, P., and D. J. Sullivan. 1982. Phenology of emergence of the spotted tentiform leafminer, *Phyllonorycter crataegella* (Lepidoptera: Gracillariidae) and its parasitoids in New York. J. N. Y. Entomol. Soc. 90 (4): 229-236.

Green, T. A., and R. J. Prokopy. 1984. Daily activity of apple blotch leafminer adults. Mass. Fruit Notes 49 (3): 19-22.

1986. Visual monitoring trap for the apple blotch leafminer moth, *Phyllonorycter crataegella* (Lepidoptera: Gracillariidae). Environ. Entomol. 15: 562-566.

Green, T. A., S. L. Butkewich, W. M. Coli, K. Leahy, and R. J. Prokopy. 1987. Monitoring and control of apple blotch leafminer: An update. Mass. Fruit Notes 52: 12-15.

Gross, P. 1986. Life histories and geographic distributions of two leafminers, *Tildenia georgei* and *T. inconspicuella*
(Lepidoptera: Gelechiidae), on solanaceous weeds. Ann. Entomol. Soc. Am. 79: 48-55.

Hagley, E. A. C., D. J. Pree, C. M. Simpson, and A. Hikichi. 1981. Toxicity of insecticides to parasites of the spotted tentiform leafminer (Lepidoptera: Gracillariidae). Can. Ent. 113: 899-906.

Haynes, K. F., and M. C. Birch. 1986. Temporal reproductive isolation between two species of plume moths (Lepidoptera: Pterophoridae). Ann. Entomol. Soc. Am. 79: 210-215.

Herbert, H. J. and K. B. McRae. 1983. Effect of temperature on the emergence of overwintering *Phyllonorycter blancardella* (Lepidoptera: Gracillariidae) and its parasite *Apanteles ornigis* (Hymenoptera: Braconidae) in Nova Scotia. Can. Entomol. 115: 1203-1208.

Hislop, R. G., and R. J. Prokopy. 1979. Integrated management of phytophagous mites in Massachusetts (U.S.A.) apple orchards: 1. Foliage inhabiting mite complexes in commercial and abandoned orchards. Prot. Ecol. 1: 279-290.

1981. Integrated management of phytophagous mites in Massachusetts (U.S.A.) apple orchards: 2. Influence of pesticides on the predator *Amblyseius fallacis* (Acarina: Phytoseiidae) under laboratory and field conditions. Prot. Ecol. 3: 157-172.

Hoyt, S. C. 1983. Biology and control of the western tentiform leafminer. Proc. Wash. State Hortic. Assoc. 79: 115-118.

Johnson, E. F., J. E. Laing, and R. Trottier. 1976. The seasonal occurrence of *Lithocoletis blancardella* (Gracillariidae) and its major natural enemies in Ontario apple orchards. Proc. Entomol. Soc. Ontario 107: 31-45.

Johnson, E. F., R. Trottier, and J. E. Laing. 1979. Degree-day relationships to the development of *Lithocoletis blancardella* (Lepidoptera: Gracillariidae) and its parasite *Apanteles ornigis* (Hymenoptera: Braconidae). Can. Entomol. 111: 1177-1184.

Laing, J. E., and J. M. Heraty. 1981. Establishment in Canada of the parasite *Apanteles pedias* Nixon on the spotted tentiform leafminer, *Phyllonorycter blancardella* (F.). Environ. Entomol. 10: 933-935.

Laing, J. E., J. M. Heraty, and J. E. Corrigan. 1986. Leaf burial by the earthworm, *Lumbricus terrestris* (Oligochaeta: Lumbricidae), as a major factor in the population dynamics of *Phyllonorycter blancardella* (Lepidoptera: Gracilariidae) and its parasites. Environ. Entomol. 15: 321-326.

1986a. Summer Diapause in *Phyllonorycter blancardella* (Fabr.) (Lepidoptera: Gracillariidae) in Ontario. Can. Ent. 118: 17-28.

Lawton, J. H. and D. R. Strong Jr. 1981. Community patterns and competition in folivorous insects. Amer. Natural. 118 (3): 317-338.

Maier, C. T. 1981. Seasonal occurrence, abundance, and leaf damage of the apple blotch leafminer, *Phyllonorycter crataegella*, in Connecticut apple orchards. Environ. Entomol. 10: 645-649.

1982. Parasitism of the apple blotch leafminer, *Phyllonorycter crataegella*, on sprayed and unsprayed apple trees in Connecticut. Environ. Entomol. 11: 603-610.

1983. Relative abundance of the spotted tentiform leafminer, *Phyllonorycter blancardella* (F.), and the apple blotch leafminer, *P. crataegella* (Clemens)(Lepidoptera: Gracillariidae) on sprayed and unsprayed apple trees in Connecticut. Ann. Entomol. Soc. Am. 76: 992-995.

1984. Abundance and phenology of parasitoids of the spotted tentiform leafminer, *Phyllonorycter blancardella* (Lepidoptera: Gracillariidae), in Connecticut. Can. Entomol. 116: 443-449.

1985. Rosaceous hosts of Phyllonorycter species (Lepidptera: Gracillariidae) in New England. Ann. Entomol. Soc. Am. 78: 826-830.

Martin, J. L. 1956. The bionomics of the aspen blotch miner, *Lithocolletis salicifoliella* Cham. (Lepidoptera: Gracillariidae). Can. Entomol. 88: 156-168.

McNeil, J. N., D. T. Quiring. 1983. Evidence of an oviposition-deterring pheromone in the alfalfa blotch leafminer, *Agromyza frontella* (Randani) (Diptera: Agromyzidae). Environ. Entomol. 12: 990-992.

Parella, M. P. 1983. Intraspecific competition among larvae of *Liriomyza trifoli* (Diptera: Agromyzidae). Ann. Entomol. Soc. Am. 78: 429-432.

Potter, D. A. 1985. Population regulation of the native holly leafminer, *Phytomyza ilicicola* Loew (Diptera: Agromyzidae), on American holly. Oecologia 66: 499-505.

Pottinger, R. P., and E. J. LeRoux. 1971. The biology and dynamics of the *Lithocolletis blancardella* (Lepidoptera: Gracillariidae) on apple in Quebec. Mem. Entomol. Soc. Can. 77. 437 pp.

Pree, D. J., E. A. C. Hagley, C. M. Simpson, and A. Hikichi. 1980. Resistance of the spotted tentiform leafminer *Phyllonorycter blancardella* to organophosphorous insecticides in southern Ontario. Can. Entomol. 112: 469-474.

Pree, D. J., D. B. Marshall, and D. E. Archibald. 1986. Resistance to pyrethroid insecticides in the spotted tentiform leafminer, *Phyllonorycter blancardella* (Lepidoptera: Gracillariidae), in southern Ontario. J. Econ. Entomol. 79: 318-322.

Prokopy, R. J. 1972. Evidence for a pheromone deterring repeated oviposition in apple maggot flies. Environ. Entomol. 1: 326-332.

1981. Epideictic pheromones that influence spacing patterns of phytophagous insects. In Semiochemicals: Their Role in Pest Control. D. A. Nordlund, ed. Wiley & Sons, Inc., N. Y. Pp. 181-213.

1985. A low-spray apple-pest-management program for small orchards. Can. Entomol. 117: 581-585.

Prokopy, R. J., B. D. Roitberg, and A. L. Averill. 1984. Resource partioning. In Chemical Ecology of Insects. W. J. Bell and R. T. Carde, eds. Chapman and Hall Ltd., London. Pp. 301-329.

Quiring, D. T., and J. N. McNeil. 1983. Exploitation and interference intraspecific larval competition in the dipteran leaf miner, *Agromyza frontella* (Rondani). Can. J. Zool. 62: 421-427.

1984. Adult-larval intraspecific competition in *Agromyza frontella* (Diptera: Agromyzidae). Can. Entomol. 116: 1385-1391.

Reissig, W. H., R. W. Weires, and C. G. Forshey. 1982. Effects of gracillariid leafminers on apple tree growth and production. Environ. Entomol. 11: 958-963.

Ridgway, N. M., and D. L. Mahr. 1985. Natural enemies of the spotted tentiform leafminer, *Phyllonorycter blancardella* (Lepidoptera: Gracillariidae), in sprayed and unsprayed apple orchards in Wisconsin. Environ. Entomol. 14: 459-463.

Roelofs, W. L., W. H. Reissig, and R. W. Weires. 1977. Sex attractant for the spotted tentiform leaf miner moth, *Lithocolletis blancardella*. Environ. Entomol. 6: 373-374.

Roitberg, B. D., and R. J. Prokopy. 1982. Resource assessment by adult and larval codling moths. J. N. Y. Entomol. Soc. 90 (4): 258-265.

Roitberg, B. D., and R. J. Prokopy. 1987. Insects that mark host plants. BioScience 37 (6): 400-406.

Schoener, T. W. 1982. The controversy over interspecific competition. Amer. Scientist. 70: 586-595.

1983. Field experiments on interspecific competition. Amer. Nat. 122: 240-285.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry, 2nd ed. W. H. Freeman and Co., NY.

Trimble, R. M. 1984. Effect of carbohydrate on the fecundity of the spotted tentiform leafminer, *Phyllonorycter blancardella* (Lepidoptera: Gracillariidae). Can. Entomol. 116: 1433-1434.

1986. Effect of temperature on oviposition and egg development in the spotted tentiform leafminer, *Phyllonorycter blancardella* (Lepidoptera: Gracillariidae). Can. Entomol. 118: 781-787.

Van Driesche, R. G., and G. Taub. 1983. Impact of parasitoids on Phyllonorycter leafminers infesting apple in Massachusetts, U.S.A. Prot. Ecol. 5: 303-317.

Van Driesche, R. G., J. M. Clark, M. W. Brooks, and F. J. Drummond. 1985. Comparative toxicity of orchard insecticides to the apple blotch leafminer, *Phyllonorycter crataegella* (Lepidoptera: Gracillariidae), and its eulophid parasitoid, *Sympiesis marylandensis* (Hymenoptera: Eulophidae). J. Econ. Entomol. 78: 926-932.

Weires, R. W. 1977. Control of *Phyllonorycter crataegella* in eastern New York. J. Econ. Entomol. 70 (4): 521-523.

1981. The bionomics and control of spotted tentiform leafminer and San Jose scale. Proc. Mass. Fruit Growers' Annu. Mtg. 86: 64-72.

Weires, R. W., and C. G. Forshey. 1978. Leafminer stages a comeback. Amer. Fruit Grower 98 (3): 26, 50.

Weires, R. W., D. R. Davis, J. R. Leeper, and W. H. Reissig. 1980. Distribution and parasitism of gracillariid leafminers on apple in the northeast. Ann. Entomol. Soc. Am. 73: 541-546.

Weires, R. W., D. R. Ophardt, and G. L. Smith. 1977. Spotted tentiform leafminer - strategies for control. Proc. N. Y. State Hortic. Soc. 122: 163-168.

Weires, R. W., J. R. Leeper, W. H. Reissig, and S. E. Lienk. 1982. Toxicity of several insecticides to the spotted tentiform leaminer (Lepidoptera: Gracillariidae) and its partasite, *Apanteles ornigis*. J. Econ. Entomol. 75: 680-684.

Wilson, H. F. 1915. An apple leaf miner, *Phyllonorycter crataegella* Clem. Second Biennial Crop Pest and Horticultural Report, 1913-14. Oregon Agric. Exp. Stn. Corvallis. pp. 119-120. (Abstract) Rev. Appl. Entomol. 3 (A): 269.